ANNALS OF THE SOUTH AFRICAN MUSEUM

ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

VOLUME 91

BAND 91

ANNALS OF THE SOUTH AFRICAN MUSEUM
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VOLUME 91 BAND

SEMPER ALIQUID NOVI AFRICA AFFERT

THE TRUSTEES OF THE
SOUTH AFRICAN MUSEUM
CAPE TOWN

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ANNALS

OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

SEMPER ALIQUID NOVI AFRICA AFFERT

INSTRUCTIONS TO AUTHORS

1. MATERIAL should be original and not published elsewhere, in whole or in part.

2. LAYOUT should be as follows:

(a) *Centred masthead to consist of*
Title: informative but concise, without abbreviations and not including the names of new genera or species
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Number of illustrations (figures, enumerated maps and tables, in this order)
(b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
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(e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
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3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

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Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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For books give title in italics, edition, volume number, place of publication, publisher.
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KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(*continued inside back cover*)

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THE SOUTH AFRICAN MUSEUM'S *MEIRING NAUDE* CRUISES
PART 13
BRYOZOA II

By

P. J. HAYWARD
&
P. L. COOK

Cape Town Kaapstad

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THE SOUTH AFRICAN MUSEUM'S *MEIRING NAUDE* CRUISES

PART 13

BRYOZOA II

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(With 33 figures, 5 tables and 2 appendices)

[*MS accepted 8 June 1982*]

ABSTRACT

The bryozoan benthos of the shallow continental shelf seas off the eastern South African coast is rich in species, and taxonomically diverse. Samples from 18 stations established by the R.V. *Meiring Naude* between 1977 and 1979 have yielded a total of 38 anascan Cheilostomata, 76 ascophoran Cheilostomata and 16 Cyclostomata. The majority of the species were collected in depths of less than 100 m. Forty-four new species are described in the following genera: *Amphiblestrum*, *Copidozoum*, *Chaperia*, *Arachnopusia*, *Micropora*, *Macropora*, *Aspidostoma*, *Bugulella*, *Beania*, *Cribrilaria*, *Smittina*, *Smittoidea*, *Parasmittina*, *Escharella*, *Mucropetraliella*, *Cleidochasma*, *Hippoporella*, *Emballotheca*, *Fenestrulina*, *Gigantopora*, *Adeonella*, *Sertella*, *Iodictyum*, *Rhynchozoon*, *Brodiella*, *Turbicellepora*, *Hornera*. Additionally, *Dactylostega* gen. nov. is introduced for several species within the Hiantoporidae.

The South African bryozoan fauna includes a high proportion of endemic species, but also exhibits a marked faunal affinity with the Indo-West-Pacific region. The antiquity of this link is suggested by a number of similarities with the Tertiary fossil faunas of Australia and New Zealand.

CONTENTS

Ann. S. Afr. Mus. **91** (1), 1983: 1–161, 33 figs, 5 tables, 2 appendices

INTRODUCTION

The first report on the Bryozoa collected by the South African Museum's *Meiring Naude* cruises (Hayward & Cook 1979) described a fauna of 51 species from a series of stations on the outer continental shelf and the continental slope of eastern South Africa. These stations ranged in depth from 376 to 1 300 m, with most of them being deeper than 500 m. A preponderance of the species was shown to comprise specialized forms adapted to life on fine-grained, unstable sediments, although a number of species were more characteristic of hard-ground benthos and were considered to have been collected at the lower limits of their bathymetric ranges. A remarkable proportion of the fauna, 23 species, was new to science and, of the remainder, 14 were new records for South Africa. The present report describes the bryozoan material collected during the *Meiring Naude* cruises of 1977, 1978, and 1979, together with an additional sample from the 1976 cruise, and provides a useful supplement to the first survey in supplying data for the inner shelf areas of the same region. Thus, of the 18 samples studied here, 8 were collected in depths of less than 100 m, 1 was collected at 150–200 m, and 6 at less than 700 m. The samples contained abundant bryozoan material and, in contrast to the first collection, which included many widely distributed deep-sea species, were expected to provide a clearer picture of the indigenous South African fauna. These expectations were exceeded when study of the collections revealed 130 species, including an astonishing total of 44 new species, many of which seem to be endemic to this area of the south-western Indian Ocean. It is now apparent that the bryozoan fauna of South Africa comprises a rich and taxonomically diverse assemblage of species, and that the few previous studies on this region (see Day *et al.* 1970) have failed to reveal more than a fraction of its potential complexity.

The bottom sediments at a number of the stations studied here included a substantial fraction of bryozoan remains. These fragments included numerous unrecognized species of Cheilostomata and Cyclostomata that could be neither identified with any of the species described here nor adequately characterized from the material available. This report, therefore, cannot be regarded as a complete survey of the shallow component of the South African bryozoan benthos. Further collections will, without doubt, produce a yet greater range of undescribed or poorly known species and genera. Many of the previously described species reported here for the first time from South African waters are known to be widely distributed in the Indo-West-Pacific region. Several of the new species have systematic affinities with Tertiary fossil forms of Australia and New Zealand. The potential of further research in this region for marine zoogeographical theory seems exciting.

LIST OF SPECIES

The present collections comprised 130 species of Bryozoa: 38 anascan Cheilostomata, 76 ascophoran Cheilostomata and 16 Cyclostomata. Ctenostomata were not found. In Tables 1–3 the species are listed in systematic order and their occurrence at each of the eighteen stations is given. The stations are arranged in order of increasing depth and the notation distinguishes between live and dead records. Co-ordinates and depths for each of the stations studied are given in Appendix 1. Data for all stations have been published by Louw (1977, 1980).

TABLE 1

Anascan Cheilostomata. The species are listed in systematic order, stations in order of increasing depth. New species are indicated by an asterisk (*). × = represented by living colonies. † = dead colonies only.

								100 m	500 m						700 m			
Depth station	179	180	184	163	163/164	164	185	239↓	250↓	234	233	232	162	103	123↓	131	129	151
Carbasea mediocris								×	×		×							
Cupuladria multispinata	†	†					†						†					
Discoporella umbellata	×	×	†		†		†						†			†		
Setosellina roulei						†								†		†		
Heliodoma implicata														×	×	†		
Callopora sp.				†	†	†	†											
Amphiblestrum inermis			×	×		†	×											
**Amphiblestrum pontifex*								×										
**Copidozoum transversum*								×	×									
Crassimarginatella marginalis				×	†	†		×	×									
Foveolaria imbricata	×	†	†	†	†		×									†	†	†
Foveolaria sp.													†					
Chaperia multifida	×	†	†	†	†		×											
Chaperia capensis	×	†			×													
Chaperia stephensoni			†	†														
**Chaperia familiaris*		×		×									×					
Chaperia sp.		†	†	†	†		†											
Notocoryne cervicornis		†	†	†	†		†											†
**Dactylostega prima*	×	×	×	×	×	×	×						×			†		
**Arachnopusia corniculata*					×	×			×							†		
**Micropora similis*		†		×	×	×		×	×		†							
Steginoporella buskii				†	×	×										†		
**Macropora africana*			×	×	×		†											
Cellaria tectiformis										×	×			†		†		†
Cellaria punctata		†			×	×												
Cellaria paradoxa														†				
**Aspidostoma livida*			†			†		×								†		
Caberea darwinii	×		×		×		×	×										
Eupaxia quadrata												×						
Menipea crispa	×				×	×												
Menipea triseriata	×	×		×		×	×											
Menipea ornata							×											
Menipea marionensis	×	×					×											
Bugulella australis											×							
**Bugulella problematica*											×							
Beania magellanica	×			×				×										
**Beania rediviva*									×									
Bugula dentata		×																
Species per station	11	14	11	15	16	12	14	8	6	1	5	1	5	4	1	9	1	3

Table 2

Ascophoran Cheilostomata. The species are listed in systematic order, stations in order of increasing depth. New species are indicated by an asterisk (*). × = represented by living colonies. † = dead colonies only.

								100 m	500 m						700 m			
Depth station	179	180	184	163	163/164	164	185	239↓	250↓	234	233	232	162	103	123↓	131	129	151
Cribrilaria innominata				×	×													
Cribrilaria venusta								×										
**Cribrilaria africana*				×		×			×									
Figularia philomela				×														
Figularia sp.				×														
Escharoides contorta		†	×	×	×	×	×	×					†					†
**Dimorphocella moderna*	†	†				†	†	×	†									
Exechonella sp.						†	†		†									
Pachycleithonia mutabilis																†	†	
Tropidozoum burrowsi																†		†
**Smittina sitella*				†	†		†	×										
**Smittina ferruginea*								×										
**Smittoidea circumspecta*			×	×			×	×										
**Smittoidea errata*					×			×										
**Smittoidea calcarata*											×							
Parasmittina tropica			×	×	†	†	†	×										
**Parasmittina novella*								×										
Porella capensis				†		×		×										
**Escharella discors*					†													
**Mucropetraliella asymmetrica*	†	†		†		×	†	×										
Arthropoma cecilii							×											
Arthropoma circinatum				†														
Arthropoma sp.				×			×											
Escharina pesanseris									×									
Escharina waiparaensis						×		×										
Calyptotheca nivea	×			×	†	×	×					×						
Calyptotheca porelliformis				×			×											
**Emballotheca ambigua*									×									
Stomachetosella balani							×											
Cleidochasma porcellanum				×														
Cleidochasma protrusum																†		
Cleidochasma cribritheca				×	×	×												
**Cleidochasma perspicua*				×														
Hippoporidra senegambiensis							×											
Hippoporella spinigera				×		×			×							†		†
**Hippoporella labiata*									×									
Hippomenella avicularis				†												†		
Microporella sp.					†			×										
Flustramorpha flabellaris	×	†																
Flustramorpha marginata			†		†		×	×										
Flustramorpha angusta			×	×	×		×									†		
**Fenestrulina indigena*				×	×													
Trypostega venusta				×	×	×		×										
Gigantopora polymorpha	×	†					×											
**Gigantopora foraminosa*			†	×	×	†										†		
Adeonella majuscula											×							
Adeonella cracens														†				
**Adeonella decipiens*	†	†	†	×	×		×									†		
**Adeonella confusanea*	×			†	×		×											
**Adeonella conspicua*	×																	
**Adeonella distincta*							×											
**Adeonella infirmata*								×										
**Adeonella abdita*				×	×	×	×	×										
**Adeonella gibba*	×	†		×	×		×											

Table 2 continued on next page.

								100 m	500 m							700 m		
Depth station	179	180	184	163	163/164	164	185	239↓	250↓	234	233	232	162	103	123↓	131	129	151
**Adeonella alia*	×																	
Tessaradoma bispiramina										×	×			†				†
Tessaradoma circella											×			†				
Sertella lata	×			×			×											
**Sertella verecunda*							×											
Schizoretepora tessellata		†		†	†		×											
Reteporella dinotorhynchus			†	†	†		×											
**Iodictyum flosculum*				†		×	×											
**Rhynchozoon documentum*				×	×	×												
**Rhynchozoon beatulum*			×	×	×		×											
**Rhynchozoon incallidum*		†	×	×	×		×											
**Rhynchozoon oscitans*		†					×											
**Rhynchozoon stomachosum*										×								
**Rhynchozoon ptarmicum*	×						×	×	×									
Brodiella longispinata							×	×										
**Brodiella ignota*									×									
Turbicellepora conica	×	†	†	†	†	×	×											
**Turbicellepora valligera*				×				×										
Celleporaria tridenticulata				†	†	†							†					
Celleporaria capensis		†		†	†		†											
Vittaticella sp.							×											
Anoteropora latirostris					×		×											
Species per station	13	12	11	38	27	18	35	20	9	2	4	1	2	3	0	8	1	4

TABLE 3

Cyclostomata. The species are listed in systematic order, stations in order of increasing depth. New species are indicated by an asterisk (*). × = represented by living colonies. † = dead colonies only.

								100 m	500 m							700 m		
Depth station	179	180	184	163	163/164	164	185	239↓	250↓	234	233	232	162	103	123↓	131	129	151
Diaperoecia				×														
Mecynoecia clavaeformis					×											×		
Mecynoecia delicatula					×		×										†	
Mecynoecia australis		†			×		×										†	†
Plagioecia patina					×													
Liripora lineata					×		×											
Idmidronea contorta					†		†									†	†	
Idmidronea crassimargo					×		×											
Idmidronea cf. *parvula*					†		†											
Idmidronea cf. *biporata*					†		†											
Idmidronea cf. *antarctica*					†											†	†	
Idmidronea cf. *atlantica*					†												†	
Crisia elongata					×										×			
Lichenopora novae-zealandiae			×		×		×									†		
Crisina radians																†		
**Hornera erugata*				†														
Species per station	0	1	1	2	13	0	8	0	0	0	0	0	0	0	1	5	5	1

SYSTEMATIC ACCOUNT

ORDER CHEILOSTOMATA

Family **Flustridae** d'Orbigny, 1852

Flustridae d'Orbigny, 1852: 324. Smitt, 1868: 357. Ryland & Hayward, 1977: 76.

Carbasea Gray, 1848

Carbasea Gray, 1848: 105, 146. Ryland & Hayward, 1977: 79.

Carbasea mediocris Hayward & Cook, 1979

Fig. 1A–B

Carbasea mediocris Hayward & Cook, 1979: 52, fig. 2A–B.

Material

Stations SM 233, SM 239, SM 250.

Remarks

The present material allows a more complete description of this species. Live colonies were obtained from each of the three stations and together include all astogenetic and ontogenetic stages. The specimens were up to 55 mm in length, the slender fronds dividing dichotomously at regular intervals; there were six to eight longitudinal series of zooids. The ancestrula (Fig. 1B) was slender and elongate and, including its tubular proximal extension, exceeded 3 mm in length. The basal portion of the colony presents a most curious appearance, with short cylindrical rhizoids projecting at right angles from the lateral borders of the ancestrula and the lowest zooids of the colony, before flexing abruptly and descending in flat fused bundles to the substratum. Most of the specimens were brooding embryos; the ovicells, partially immersed in the zooids distal to the maternal zooids, were up to 0,46 mm long and equally broad, thinly calcified with a faintly striated surface.

The holotype was collected from 550 m depth (Hayward & Cook 1979), the present material was obtained at depths of 90 m to 580 m.

Family **Cupuladriidae** Lagaaij, 1952

Cupuladriidae Lagaaij, 1952: 31. Cook, 1965*a*: 154; 1965*b*: 192.

Cupuladria Canu & Bassler, 1919

Cupuladria Canu & Bassler, 1919: 77. Lagaaij, 1952: 32. Cook, 1965*b*: 197.

Cupuladria multispinata (Canu & Bassler, 1923)

Cupularia multispinata Canu & Bassler, 1923: 78, fig. 13H.
Cupuladria multispinata: Cook, 1965*b*: 210, pl. 2 (fig. 2A–B), fig. 2d.

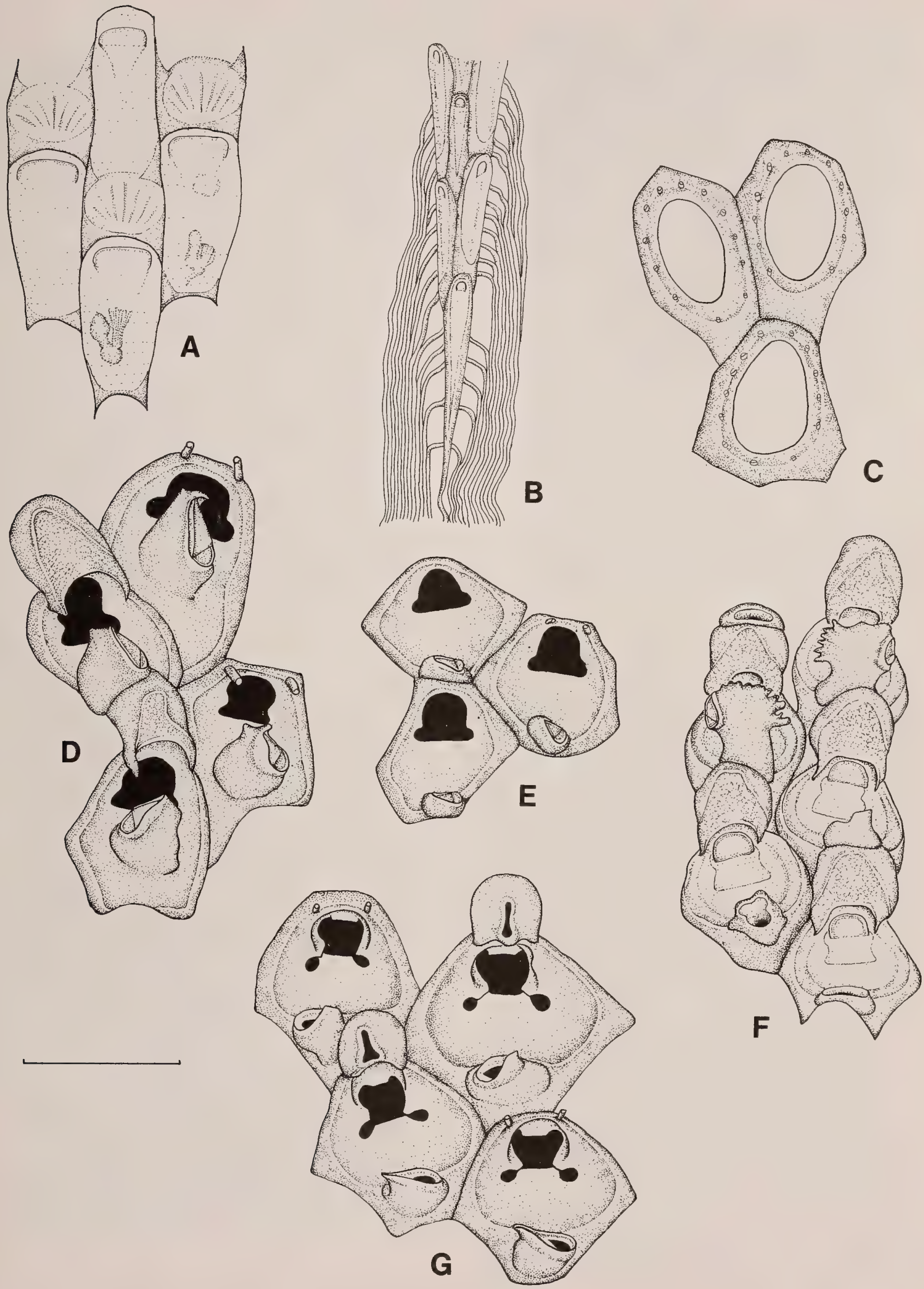

Fig. 1 A–B. *Carbasea mediocris* Hayward & Cook. A. Ovicelled zooids. B. The ancestrula, and basal attachment rhizoids. C. *Callopora* sp. D–F. *Amphiblestrum inermis* (Kluge). D. A group of zooids with large avicularia, including two with characteristic ovicells. E. Zooids from a juvenile colony, with small avicularia. F. Ovicelled zooids, two with distinctive avicularia. G. *Amphiblestrum pontifex* sp. nov. Scale = 0,5 mm for C–G; 1 mm for A–B.

Material

Stations SM 162, SM 179, SM 180, SM 185.

Description

Cupuladria with large zooids (Lz 0,55–0,76 mm). Colonies with coarsely tuberculate, alternating, radiating ridges basally. Zooids with well-developed lateral cryptocyst denticles that end in fine spinules.

Remarks

All the colonies found were dead and worn; they were almost certainly transported. *C. multispinata* differs from *C. owenii* (Gray), which also occurs in South African waters (Cook 1965*b*: 213), in its larger colonies and larger zooids. The denticulation on the edge of the cryptocyst and the basal tuberculations are also coarser than in *C. owenii*.

Distribution

North-west, west, and south-east Africa, 7–105 m.

Discoporella d'Orbigny, 1852

Discoporella d'Orbigny, 1852: 472. Cook, 1965*b*: 219.

Discoporella umbellata (Defrance, 1823)

Fig. 2

Lunulites umbellata Defrance, 1823: 361, pl. 47 (fig. 1a–b).
Discoporella umbellata: Cook, 1965*a*: 177, pl. 1 (fig. 7), pl. 3. (figs 1, 3, 5–6), fig. 4; 1965*b*: 221, pl. 3 (fig. 3), fig. 2h. Hayward & Cook, 1979: 44.

Material

Stations SM 131, SM 162, SM 163/164, SM 179, SM 180, SM 184, SM 185.

Description

Zooids with complete cryptocyst lamina, pierced by several pairs of opesiules, and other foramina. Opesia D-shaped, straight proximally. Basal surface with irregular pores or pits, becoming flat and smooth. At colony maturity a layer of kenozooids alternating with avicularia grows from the periphery and spreads over the basal surface, which is usually by then flat, not curved.

Remarks

Most populations of *D. umbellata* do not show the basal changes that occur in these specimens. This morphotype was described as '*D. umbellata peyroti*-type' by Cook (1965*a*: 179), because a similar form of colony growth

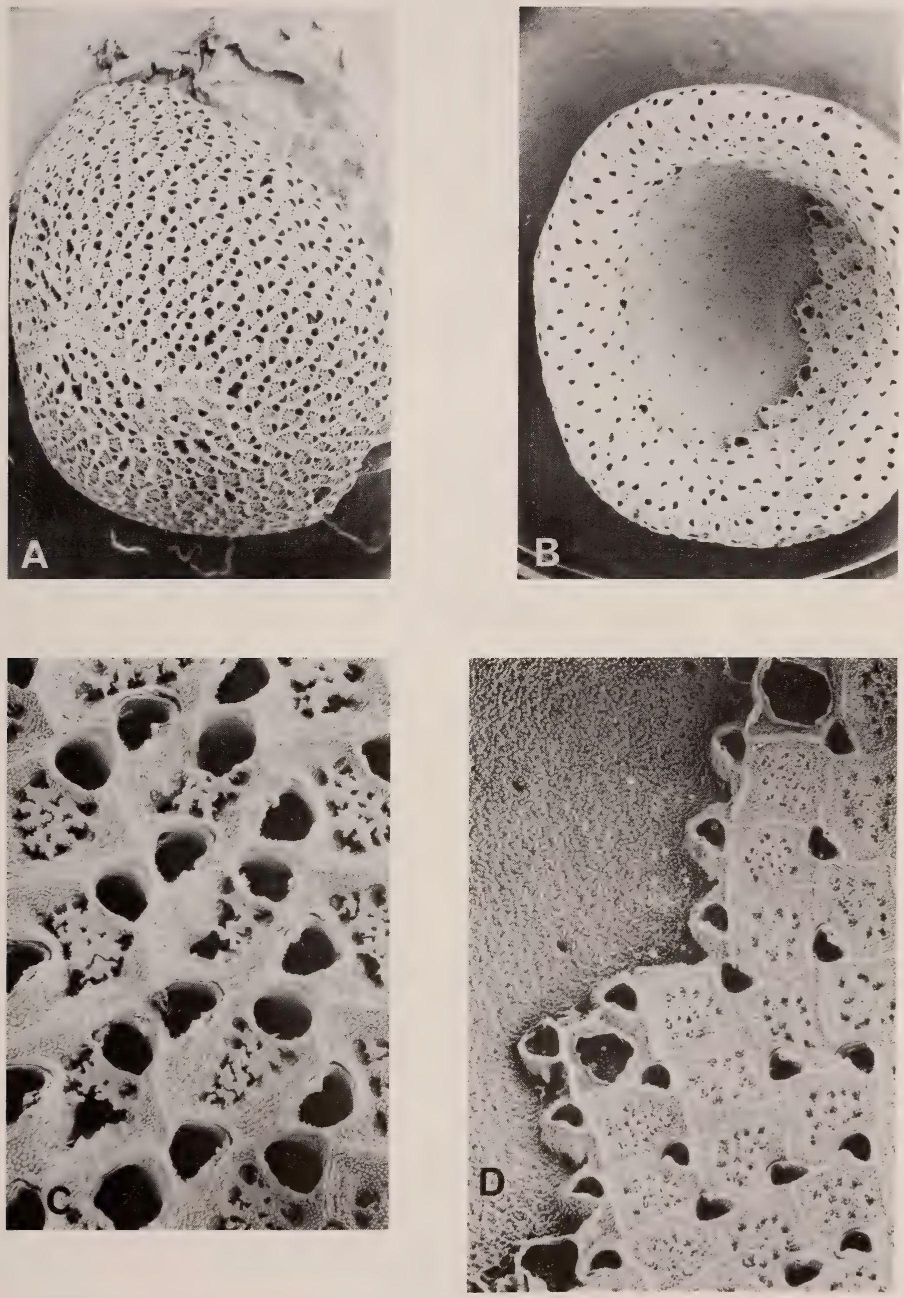

Fig. 2. *Discoporella umbellata* (Defrance). A. Frontal view of a colony. × 9,3. B. Basal view showing the ingrowing layer of kenozooids and avicularia. × 9,3. C. Enlarged frontal view of autozooids. × 61. D. Enlarged view of basal lamina. × 26.

was first described as *Cupularia peyroti* from the European Tertiary. The cause of the progressive infilling of the concave basal surface in these colonies is unknown, but may be similar to that which produces infilling in many colonies of *C. doma* (see Cook 1965*b*: 216). The development of a basal layer of kenozooids and avicularia, however, seems to occur only in Recent populations of *D. umbellata* from South Africa. One of the functions of the basal avicularia appeared to be to discourage the settlement of larvae of sponges, serpulid worms and other bryozoans, all of which are often found occupying the basal concavity in other populations of *D. umbellata*, and in other species of the Cupuladriidae (see Cook 1965*b*: 195). Very young dead colonies were present at nearly all stations, but living colonies with avicularian setae intact were collected only at Stations SM 179 and SM 180.

Distribution

The *D. umbellata* species complex has a wide distribution in tropical and subtropical regions of the Atlantic Ocean and the western Indian Ocean, but '*peyroti*-type' colonies are known only from South Africa.

Family **Setosellinidae** Hayward & Cook, 1979

Setosellinidae Hayward & Cook, 1979: 45.

The family was introduced for genera with free-living colonies of spirally-budded zooids supported by long setiform avicularian mandibles. The zooidal opesia is extensive, and large ovicells are present.

Setosellina Calvet, 1906

Setosellina Calvet, 1906: 157. Hayward & Cook, 1979: 48.

Setosellina roulei Calvet, 1906

Setosellina roulei Calvet, 1906: 157; 1907: 395, pl. 26 (figs 5–6). Hayward & Cook, 1979: 48, figs 1A, 17B, 18B.

Material

Stations SM 103, SM 131, SM 164.

Remarks

In contrast to the large number of specimens previously reported (Hayward & Cook 1979), a very few 'dead' colonies were found in the present collections.

Heliodoma Calvet, 1906

Heliodoma Calvet, 1906: 157. Hayward & Cook, 1979: 50.

Heliodoma implicata Calvet, 1906

Heliodoma implicata Calvet, 1906: 157; 1907: 396, pl. 26 (figs 7–9). Hayward & Cook, 1979: 50, figs 17A, 18A.

Material

Stations SM 103, SM 123, SM 131.

Remarks

Some of the specimens from stations SM 103 and SM 123 were alive when collected; only those from SM 103, which have been reported before (Hayward & Cook 1979) were numerous.

Family **Calloporidae** Norman, 1903

Calloporidae Norman, 1903: 587. Ryland & Hayward, 1977: 87.

Callopora Gray, 1848

Callopora Gray, 1848: 109, 146. Ryland & Hayward, 1977: 87.

Callopora sp.

Fig. 1C

Material

Stations SM 163, SM 163/164, SM 164, SM 185.

Description

Colony encrusting. Zooids 0,5–0,7 mm long by about 0,4 mm broad. Opesia oval, cryptocyst narrow; gymnocyst smooth, of variable extent. Spines distributed around whole of opesia, up to ?12 in number. No sessile avicularia. Ovicell small, hyperstomial, perhaps with frontal area.

Remarks

Colonies of an unrecognized species of *Callopora* were found at each of the above stations. All were dead, and damaged to a greater or lesser extent. Although it appears to be undescribed, the poor state of the material precludes the possibility of an adequate taxonomic description and, accordingly, the species must remain unnamed until further specimens are collected.

Amphiblestrum Gray, 1848

Amphiblestrum Gray, 1848: 103. Ryland & Hayward, 1977: 103.

Amphiblestrum inermis (Kluge, 1914)

Fig. 1D–F

Membranipora inermis Kluge, 1914: 663, pl. 34 (fig. 6).
Lepralia triangularis O'Donoghue, 1924: 43, pl. 2 (figs 11– 12).
Amphiblestrum triangulare: O'Donoghue, 1957: 74.

Material

Stations SM 163, SM 164, SM 184, SM 185.

Description

Colony encrusting, unilaminar. Zooids flat, hexagonal or irregularly polygonal, separated by shallow grooves; 0,4–0,5 mm long by 0,36–0,4 mm broad. Cryptocyst flat, occupying half length of zooid, surrounded by a thin crenellated rim; two widely spaced, evanescent spines distally; opesia trifoliate, proportions variable, most frequently with proximal portion constituting one-third or less of total length. Gymnocyst smooth, largely obscured by a single adventitious avicularium, orientated transversely and acute to frontal plane. Rostrum hooked, supporting an acute triangular mandible. Ovicell prominent, recumbent on succeeding zooid, with a large triangular area of uncovered granular, entooecium frontally; raised border between entooecium and ectooecium produced at proximolateral corners of ovicell to form projecting, proximally directed spikes. Within the colony the size of the avicularian cystid varies astogenetically and the proportions of the opesia vary ontogenetically.

Remarks

O'Donoghue (1924) noted that his *L. triangularis* seemed similar to the Antarctic *Membranipora inermis* Kluge. The type specimen (BMNH 1963.3.20.7.) is poor, consisting of fragments of several young colonies; there are no ovicells and most of the zooids lack avicularia. A second specimen from Saldanha Bay (BMNH 1936.12.30.281) is equally fragmentary, but the zooids possess avicularia. It is difficult, therefore, to identify O'Donoghue's material with *M. inermis* Kluge. Good examples of the latter species are known from South Africa, viz. from False Bay (BMNH 1962.6.4.6.), and from Simon's Bay (BMNH 1944.1.8.186); both are well-grown colonies with prominent avicularia, and the False Bay specimen has numerous ovicells showing the triangular, granular frontal area, and proximolateral processes, characteristic of Kluge's species. Unfortunately neither includes early astogenetic stages and it is not possible to judge whether the fragmentary specimens of O'Donoghue represent simply early astogenetic stages of *M. inermis*.

The *Meiring Naude* material provides some evidence for this supposition, but the number of specimens is small and additionally suggests an even broader range of variation. The material described above (station SM 184, Fig. 1D) is without doubt closest to Kluge's species, and includes some early zooids with

very small frontal avicularia. A specimen from station SM 163 (Fig. 1E), small and lacking ovicells, has very small avicularia and the zooids resemble closely both the early astogenetic stages of the colony from SM 184 and O'Donoghue's type specimen of *L. triangularis*. In a specimen from station SM 185 (Fig. 1F) the free distal edge of the avicularian cystid is flattened and expanded, forming a structure similar to that seen in species of *Foveolaria*; however, the ovicell, the paired spines, the opesia, and the avicularian rostrum are identical to those of the material described (SM 184).

Amphiblestrum pontifex sp. nov.

Fig. 1G

Material

Holotype: SAM–A26413, station SM 239, 32°14,8′S 29°00,8′E, 90 m.

Description

Colony encrusting. Zooids oval, broad and flat, distinct, separated by deep grooves. Gymnocyst reduced but visible, continuous laterally with incurved lateral walls, smooth and hyaline. Cryptocyst extensive, comprising four-fifths of total zooid length, flat and smooth, encircled by a raised and thickened mural rim. Opesia subterminal, less than half length of cryptocyst, and distally less than half its width; shape characteristic, opesiular indentations small, initially continuous with distal part of opesia, but later isolated from it. Two widely spaced distal oral spines present in newly developed zooids, later lost. Avicularium medially situated on gymnocyst, orientated transversely; cystid globose, rostrum elongate, acute-triangular, its distal end curved to left or right. Ovicell prominent, spherical, small; smooth surfaced, with a longitudinal median ridge marking the thickened edges of a narrow frontal foramen.

Etymology

Pontifex (L.)—high priest, an allusion to the shape of the opesia.

Remarks

A. pontifex may be distinguished from other species of *Amphiblestrum* by the form of the opesia, in particular by the isolation of the opesiular indentations. Several live colonies encrusting the large specimen of *Dimorphocella* were collected.

Measurements (means of 20 values) in mm

Lz	lz
0,57	0,48

Copidozoum Harmer, 1926

Copidozoum Harmer, 1926: 226.

Copidozoum transversum sp. nov.

Fig. 3A

Material

Holotype: SAM–A26414, station SM 239, 32°14,8′S 29°00,8′E, 90 m.
Other material: station SM 250.

Description

Colony encrusting. Zooids oval, large. Frontal surface almost entirely membranous: gymnocyst apparent as a small triangular area of calcification on zooids at a row bifurcation; cryptocyst forming simply a narrow granulated border, mural rim thin, no spines. Vicarious avicularia conspicuous, cystid tumid; rostrum orientated transversely, 0,24–0,34 mm long, distal portion slender, with a blunt tip, proximal portion rounded, opesia oval, with a granular cryptocyst, mandible articulating against paired, thickened condyles. Ovicells not found.

Etymology

Tranversus (L.)—crosswise, referring to the orientation of the avicularium.

Remarks

Living colonies were collected from both the above stations.

Measurements (means of 20 values) in mm

Lz	lz
0,64	0,42

Crassimarginatella Canu, 1900

Crassimarginatella Canu, 1900: 369. Hastings, 1945: 69.

Crassimarginatella marginalis (Kirkpatrick, 1888)

Fig. 3B

Membranipora marginalis Kirkpatrick, 1888: 74, pl. 7 (fig. 2).
Crassimarginatella marginalis: Hastings, 1945: 78, fig. 2B.

Material

Stations: SM 163, SM 163/164, SM 164, SM 239, SM 250.

Remarks

In the size of the zooids, the relatively broad cryptocyst, and the morphology of the vicarious avicularia, the *Meiring Naude* specimens closely resemble the Mauritian type specimen of *C. marginalis* (BMNH 1888.12.5.8.). The *Meiring Naude* specimens tend to be more thickly calcified, but as no live

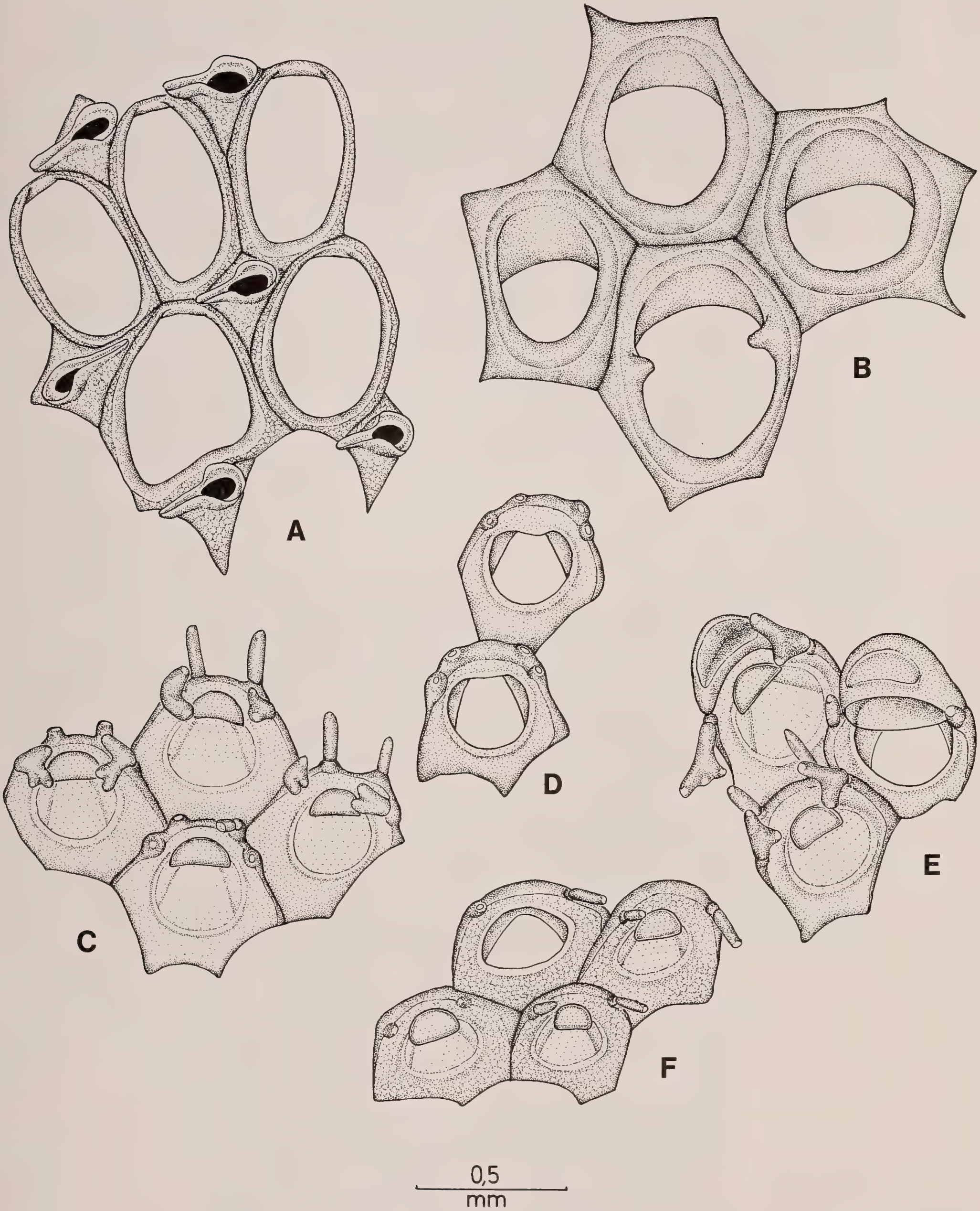

Fig. 3. A. *Copidozoum transversum* sp. nov. B. *Crassimarginatella marginalis* (Kirkpatrick). C–E. *Chaperia familiaris* sp. nov. C. Zooids from a live collected colony, showing the forked proximal spines. D. Two dead zooids, showing the extent of the occlusor laminae. E. A group of zooids with ovicells in different stages of development. F. *Chaperia capensis* (Busk).

juvenile colonies were collected, the majority of the material representing dead colonies, this may be regarded as an ontogenetic effect.

Foveolaria Busk, 1884

Foveolaria Busk, 1884: 68. Harmer, 1926: 246.

Foveolaria imbricata (Busk, 1884)

Fig. 4

Amphiblestrum imbricatum Busk, 1884: 65, pl. 15 (fig. 3).
Membranipora imbricata: Marcus, 1922: 16, fig. 9.

Material

Stations SM 129, SM 131, SM 151, SM 163, SM 163/164, SM 179, SM 180, SM 184, SM 185.

Description

Colony arising from an encrusting sheet of zooids, forming an erect cylindrical growth. Zooids in alternating linear series around the entire axis of the branch; broadly diamond-shaped, as wide as long, distal edge raised and distinctly crenellated. Frontal membrane underlain by a smooth, extensive cryptocyst, deeply concave; opesia subtriangular, occupying less than one-third of total zooid length. Frontal surface largely hidden by a tall, broad avicularium, developed on the proximal half of the cryptocyst; cystid cylindrical at first, broadened distally, with a thin irregular edge. Rostrum situated on the lateral face of the cystid, acute triangular, apically orientated, with stout condyles for articulation of the mandible. No spines. Ovicells not observed.

Remarks

Busk's original description of this species (1884: 65) is confusing. He considered he was viewing a unilaminar colony encrusting another, erect, bryozoan species, although his material is clearly an erect cylindrical colony. The relative proportions of gymnocyst and cryptocyst, the origin of the frontal avicularium, the nature of the ovicell and, perhaps, colony form are the features most likely to prove useful in distinguishing *Foveolaria* (as defined by Levinsen 1909: 152) from *Amphiblestrum* (above). At present *A. imbricata* Busk seems more correctly placed in *Foveolaria* than in *Amphiblestrum*.

Foveolaria sp.

Fig. 5A

Material

Station SM 162.

Description

Colony erect, cylindrical, slender. Zooids in triple whorls, elongate, rounded distally, tapered proximally; lateral walls flared distally, forming an

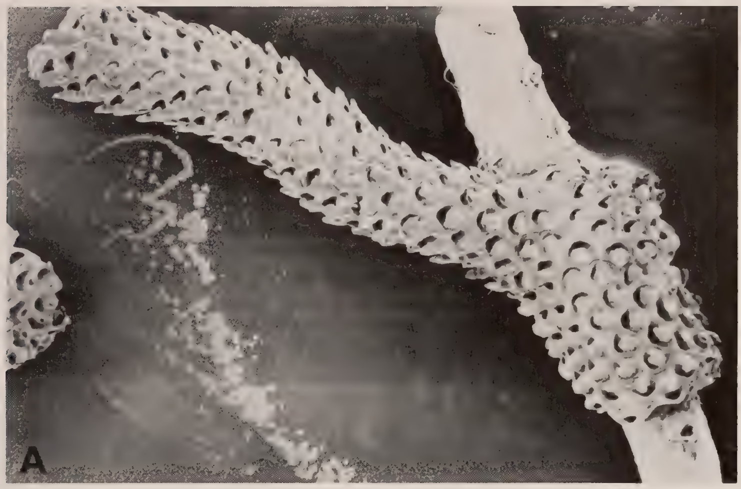

Fig. 4. *Foveolaria imbricata* (Busk). A. An entire colony. × 12. B. Detail to show the avicularia. × 82.

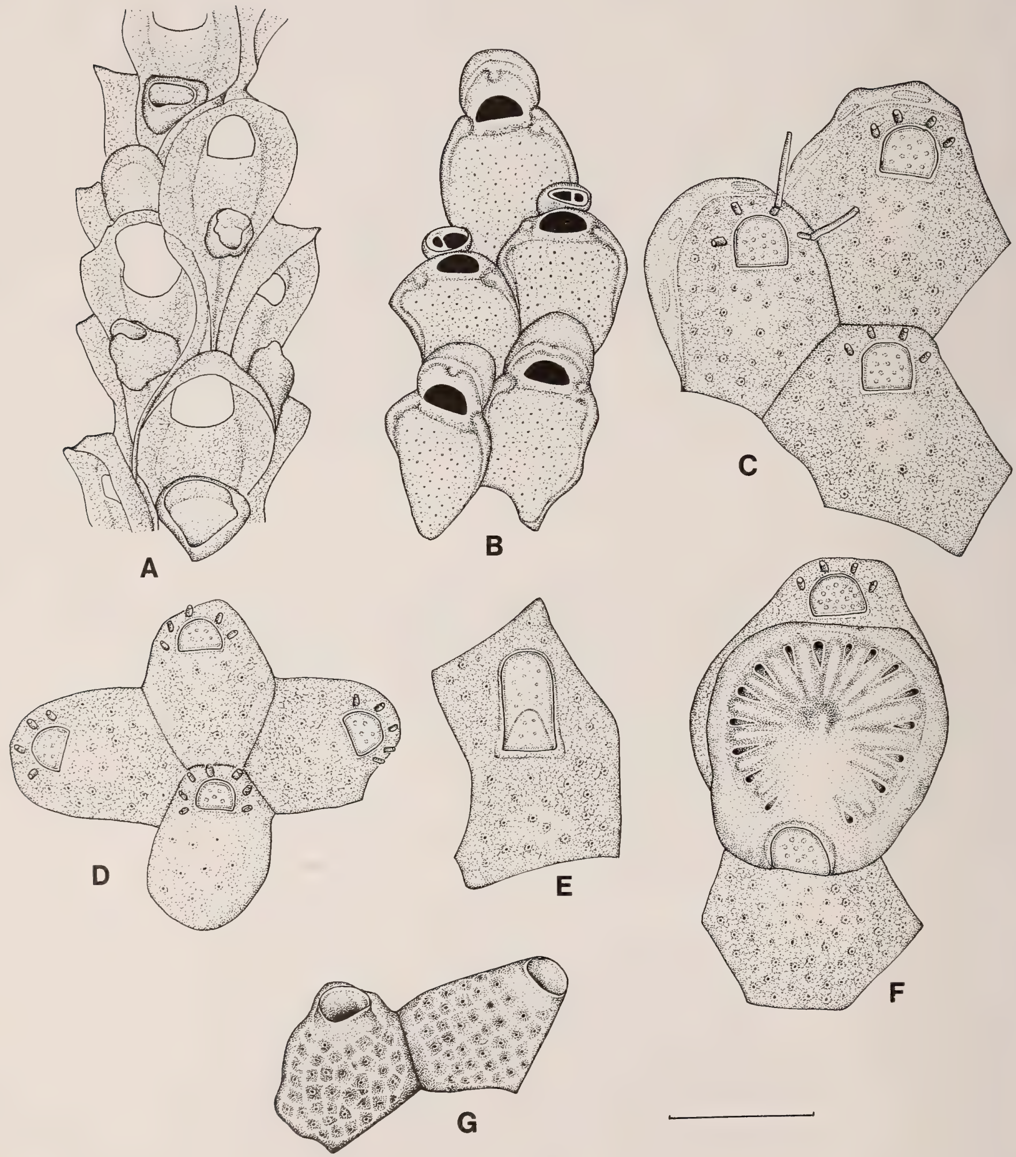

Fig. 5. A. *Foveolaria* sp., the dead specimen from SM 162. B. *Micropora similis* sp. nov. C–F. *Macropora africana* sp. nov. C. Zooids from the growing edge. D. The ancestrula, and periancestrular zooids. E. A vicarious avicularium. F. An ovicelled zooid. G. *Exechonella* sp. Scale = 0,5 mm for A–F; 1 mm for G.

arched hood. Cryptocyst extensive, flat, opesia comprising less than one-quarter of zooid length. A broad-based, possibly cylindrical, avicularian cystid present on the proximal region of the cryptocyst. Ovicell spherical. No spines.

Remarks

Dead fragments of an unrecognized species of *Foveolaria* were obtained from station SM 162. Unfortunately all of the features of the zooids were damaged to a greater or lesser extent, in particular the larger part of each avicularium was missing; the condition of the material thus precludes a complete description of the species.

Family **Chaperiidae** Jullien, 1888

Chaperiidae Jullien, 1888: 61. Brown, 1952: 94.

Chaperia Jullien, 1881

Chaperia Jullien, 1881: 163. Brown, 1952: 94. Gordon, 1982.

The genus *Chaperia* comprises a large number of species described from localities throughout the southern hemisphere. The synonymy of many of these species is confused to the extent that no useful comments may be made regarding systematic relationships or distributional patterns until the majority of described species has been critically re-examined. Brown (1952: 94) clarified the status of *Chaperia* Jullien, noting that the type species was the originally designated *C. australis* Jullien, 1881, and selected a neotype for *C. acanthina* (Lamouroux, 1825). Brown also indicated that *C. acanthina* may prove to be a senior synonym of *C. australis*, and it would seem useful to consider here whether this synonymy may be accepted.

Jullien (1881: 163) introduced *C. australis* as a new name for *Membranipora spinosa* Busk, 1879; Busk had referred his material (from Kerguelen) to *Flustra acanthina* (Lamouroux, 1825) but had derived the name from the non-Linnean 'Flustra épineuse' used by Lamouroux in the explanation of his plate (1825, Atlas, pl. 89, figs 1–2). Although Jullien (1881) was describing specimens of *C. australis* from South Africa, he was quite explicit in introducing the name for Busk's Kerguelen material, and the possible synonymy of *C. acanthina* and *C. australis* thus depends on the identity of Busk's specimens. Jullien's South African specimens pose another problem. Marcus (1922) described material from South Africa under the name *C. acanthina* var. *australis* Jullien, which is here referred to *C. capensis* (Busk) (q.v.). The South African material of *C. australis* may prove to be identical to Busk's Kerguelen specimens, or it may be identifiable with Marcus's material; only examination of Jullien's specimens will decide the issue, but its result is irrelevant to the identity of *C. australis*, which is determined solely by the Busk specimen from Kerguelen. Fortunately this is still extant (BMNH 1899.7.1.1155, 1156); it comprises a single, well-grown young colony encrusting a small rhodophyte.

Comparison with the neotype of *C. acanthina* (BMNH 1930.1.16.26A) and with other material from the Falkland Islands (BMNH 1935.3.6.59, 316) shows that Busk's specimen may be assigned confidently to *C. acanthina* (Lamouroux). The zooids of all four specimens are of a similar size (0,5–0,6 mm long by 0,4–0,5 mm broad) with a granular cryptocyst comprising two-fifths of the total length. The opesia is surrounded by jointed spines of variable thickness, up to 0,6 mm long; these number five or six on the Falkland Islands specimens, and six or seven in the Kerguelen colony. The occlusor laminae in all cases are distinct, slightly curved but not converging markedly towards the distal end of the zooid, the visible length being 0,2 mm.

It may be shown, therefore, that *C. australis* Jullien is a junior subjective synonym of *C. acanthina* (Lamouroux), which accordingly becomes the type species of *Chaperia* Jullien. The subsequent synonymy of *C. acanthina* is adequately provided by Brown (1952: 95); *C. acanthina* was also discussed by Harmer (1926: 229), but his material included the Siboga specimens from the tropical East Indies which appear to differ from Brown's neotype, most notably in possessing up to ten small spines. Finally, and inexplicably, Jullien (1888) figured specimens of a *Chaperia* from Cape Horn which he attributed to '*Flustra spinosa*', noting that it was the same as that to which he had in 1881 given the name *Chaperia australis*. His text, though brief, suggests that he had by then concluded that *C. acanthina* and *C. australis* were identical, but his use of the spurious '*Flustra spinosa*' perhaps served to obscure his opinion.

Chaperia multifida (Busk, 1884)

Fig. 6

Membranipora galeata var. *multifida* Busk, 1884: 64.
Chaperia multifida: Kluge, 1914: 673, text-fig. 44. Marcus, 1922: 7, fig. 3.
Membranipora galeata var. *multifida:* O'Donoghue & De Watteville, 1935: 205.

Material

Stations SM 163, SM 163/164, SM 179, SM 180, SM 184, SM 185.

Description

Colony encrusting, forming patches or cylindrical growths around erect substrata; developing as erect bilaminar sheets or solid branching cylinders. Zooids hexagonal or irregularly oval, separated by indistinct sutures, 0,44–0,65 mm long by 0,26–0,4 mm broad. Cryptocyst forming a narrow, finely granular, concave rim, most prominent proximally and tapering rapidly towards spine bases. Opesia circular or oval, marginally longer than wide in the larger zooids, occupying three-fifths to three-quarters of total frontal length. Occlusor laminae distinct, quite divergent distally; arising on each side from a point below the distal spine and extending to half-way along the lateral margin of the opesia. Two pairs of distolateral spines, thick, jointed at base with a distinct coelomic cavity; proximalmost pair broadening rapidly, developed as multi-branched palmate structures arching over and obscuring most of the frontal

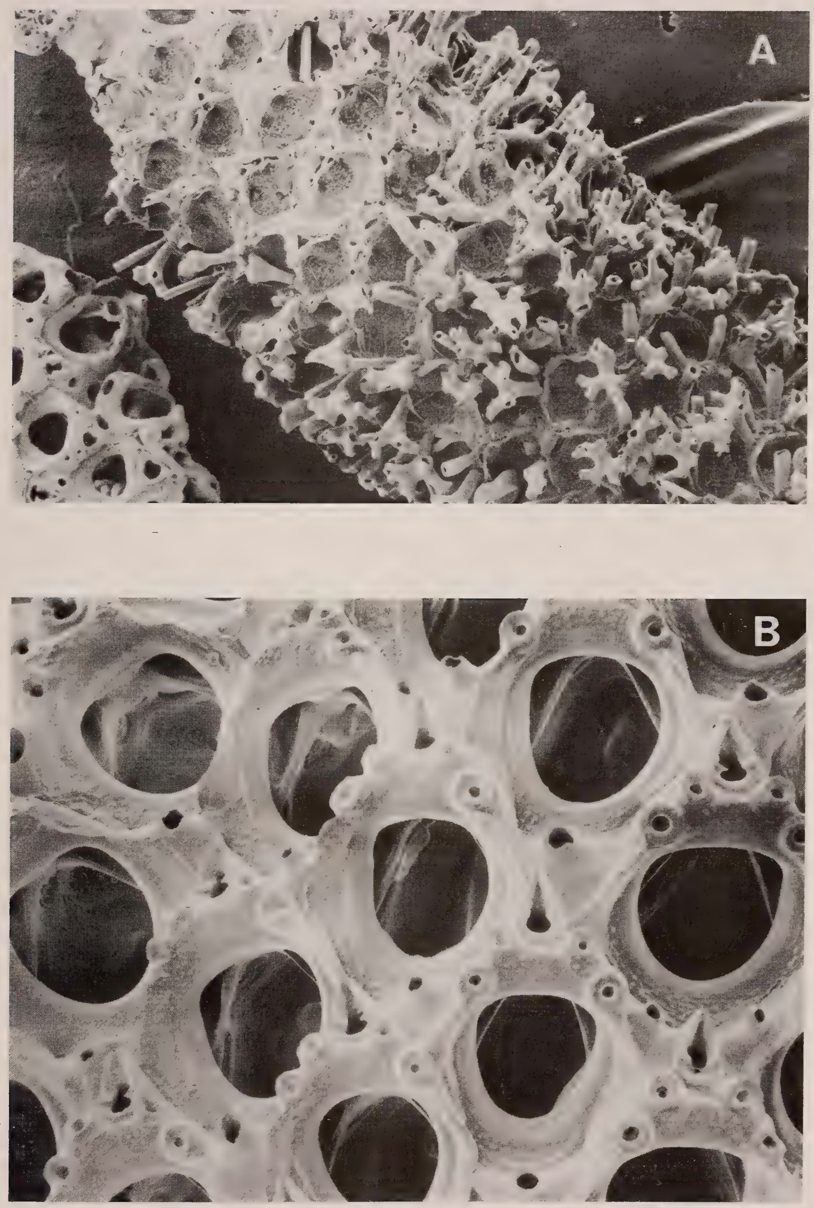

Fig. 6. *Chaperia multifida* (Busk). A. Portion of a live collected colony (on right) with spines and pedunculate avicularia intact, and a dead fragment for comparison (on left). × 29. B. Bleached fragment of a live collected colony. × 79.

surface of the zooid. Distalmost pair of spines typically erect, cylindrical, clavate or spatulate, rarely palmate. A single sessile avicularium at the distal end of each zooid, situated between the distalmost pair of spines; rostrum triangular, distally orientated, with an incomplete cross-bar and a transversely oval foramen in the palate; rarely, the rostrum may be broadened to give a narrowly spatulate shape. Erect, elongate pedunculate avicularia numerous, most frequently situated adjacent to the sessile avicularium on one or both sides; sometimes developed between adjacent zooids, arising from the lateral wall of one of them; one or more of the distal spines may also be replaced by pedunculate avicularia. Ovicell prominent, hemispherical, with an oval or irregular frontal area; in fertile zooids the distal pair of spines and the avicularia are suppressed.

Remarks

The material from SM 179 and SM 185 comprised living colonies retaining a reddish coloration in alcohol and forming cylindrical growths around hydroid stems. All the material from the other stations consisted of dead fragments; some of these were encrusting, unilaminar patches and some bilaminar sheets, but the majority were fragments of cylindrical or flattened branching colonies up to 10 mm high. Bleached zooids from SM 179, lacking spines and pedunculate avicularia are compared with those of a dead cylindrical fragment in Figures 6A–B, and it may be seen that, despite the variation in colony morphology, only one species is represented.

Chaperia capensis (Busk, 1884)

Fig. 3F

Amphiblestrum capense Busk, 1884: 67, pl. 23 (fig. 3).
Chaperia acanthina var. *australis:* Marcus, 1922: 6, fig. 2.
Membranipora galeata var. *inermis* O'Donoghue, 1924: 38, pl. 1 (fig. 9).
Chapperia acanthina var. *australis:* O'Donoghue & De Watteville, 1944: 415.

Material

Stations SM 163/164, SM 179, SM 180.

Description

Colony encrusting, forming cylindrical growths around erect substrata, developing as erect, solid cylindrical structures, branching irregularly. Zooids broad and flat, typically hexagonal, broader than long, separated by shallow grooves; 0,5–0,6 mm long by about 0,6 mm broad. Cryptocyst finely granular, concave, broadest proximally, narrowing towards the distal end. Opesia transversely oval, occupying about three-fifths of total frontal length; occlusor laminae well developed and distinct, seen to converge distally even in unbleached undamaged material, extending lateroproximally almost to the proximal edge of the opesia. One short cylindrical spine present at each distal

corner, variable in length but typically no longer than the width of the opesia. Avicularia and ovicells absent.

Remarks

The proportions of the zooids seem to vary according to the form of growth of the colony; in regular cylindrical branches they tend to be longer than broad, but may broaden considerably in encrusting sheets or irregular branches. The type material from Simon's Bay, South Africa consists of several solid cylinders lacking bases. The specimens from *Meiring Naude* stations SM 163/164 and SM 179 form hollow cylinders around hydroids; dead fragments from SM 180 consisted mostly of solid cylinders, but some included a hollow, encrusting cylindrical base.

The material described and figured by Marcus (1922: 6, fig. 2) as *C. acanthina* var. *australis* clearly belongs in the synonymy of *Chaperia capensis*; however, as discussed above, the identity of Jullien's (1881) South African records of *C. australis* can be decided only by examination of his specimens. *C. acanthina* var. *polygonia* Kluge (1914: 676, text-fig. 47), from Simon's Bay, placed by Marcus (1922) in the synonymy of his *C. acanthina* var. *australis*, differs from *C. capensis* in possessing five or six distal oral spines and widely divergent occlusor laminae. It is probably correctly regarded as a variant of *C. acanthina*.

Chaperia stephensoni O'Donoghue & De Watteville, 1935

Chaperia stephensoni O'Donoghue & De Watteville, 1935: 205, pl. 5 (fig. 1), pl. 6 (fig. 11). O'Donoghue, 1957: 74.

Material

Stations SM 163, SM 184.

Remarks

Only small dead fragments of this species were recovered. *C. stephensoni* may be recognized by the transversely oval opesia overarched by the distal wall of the zooid, and by the single distal avicularium, which has a characteristic elongate lanceolate rostrum curved slightly to the left or right at its tip. Two spine bases are visible at each distal corner and the sessile avicularium is often flanked on one or both sides by the swollen bases of erect avicularia.

Chaperia familiaris sp. nov.

Figs 3C–E, 7A

Material

Holotype: SAM–A26415, station SM 162, 32°55′S 28°31′E, 630 m.
Other material: stations SM 163, SM 180.

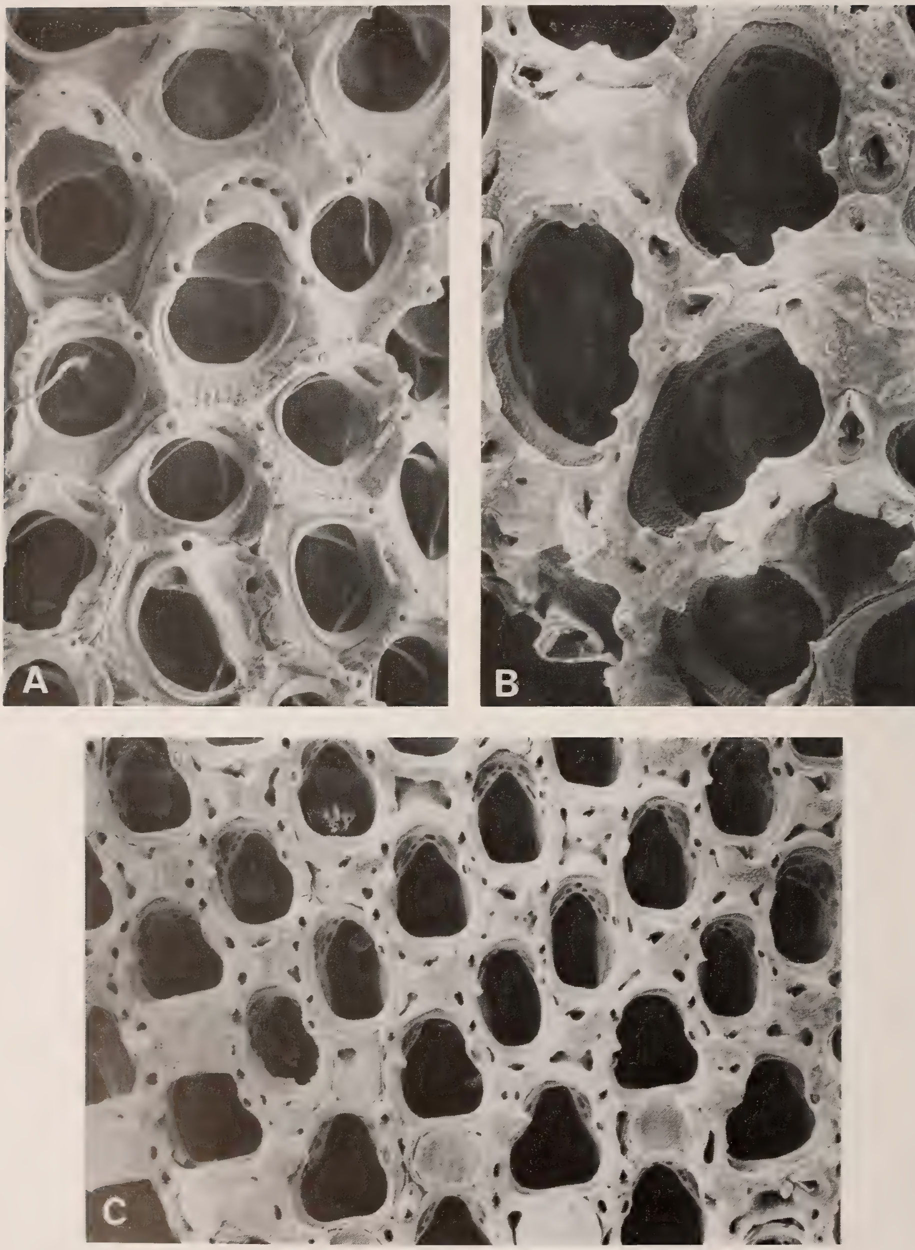

Fig. 7. A. *Chaperia familiaris* sp. nov. × 48. B. *Dactylostega prima* sp. nov. × 64. C. *Dactylostega tubigera* (Busk), BMNH 1887.12.9.3462. × 24.

Description

Colony encrusting, forming small patches, retaining a reddish-brown colour when preserved in alcohol, but fading when dried. Zooids hexagonal, occasionally rounded distally, typically as wide as long, but tending to broaden, separated by distinct sutures. Cryptocyst flat, finely granular, forming a symmetrical plate of constant width around two-thirds of the periphery of the opesia between the proximalmost pair of spines, its free edge distinctly bevelled. Opesia transversely oval, occupying approximately half the length of the frontal surface. Occlusor laminae distinct, each extending from a point one-third of the distance along the distal wall to the proximolateral corner of the zooid; not markedly convergent distally, although in damaged zooids they may be seen to join distally at the mid-line of the zooid. Two pairs of distolateral spines, distinctly shorter than the length of the opesia; distal pair cylindrical, proximal pair forked and slightly incurved. In brooding zooids only the proximal pair is present. Ovicell prominent, broader than long, hemispherical or somewhat irregular; ectooecium with a transversely oval frontal foramen. No avicularia.

Etymology

Familiaris (L.)—familiar, an allusion to the morphological features characteristic of the genus.

Remarks

Live specimens were obtained from all three stations, those from SM 162 and SM 180 were encrusting the large arenaceous foraminiferan *Schizammina pinnata* (Pearcey) (see p. 144). *C. familiaris* seems to be most similar to *C. capensis* (above) but differs in possessing two pairs of spines, most particularly in the short, forked proximal pair, and in its very characteristic ovicells.

Measurements (means of 10 values) in mm

Lz	lz	Lop	lop
0,48	0,47	0,30	0,31

Chaperia sp.

Fig. 9A

Material

Stations SM 163, SM 163/164, SM 180, SM 184, SM 185.

Description

Colony forming unilaminar sheets, encrusting or possibly erect, or only loosely attached to substratum. Zooids flat, typically broader than long, tapered proximally and rounded distally, 0,6–0,9 mm long by 0,7–1,0 mm

broad. Cryptocyst flat or slightly depressed distally, granular; opesia transversely oval, comprising up to two-thirds total length of zooid, no occlusor laminae visible. Distal border of zooid with seven to nine closely spaced spine bases. No avicularia or ovicells. Vertical walls very deep, up to 1,0 mm in some fragments; in basal view zooid boundaries are marked by distinct ridges. Both vertical and basal walls densely perforated by large multiporous septula, each in a distinct pit.

Remarks

Detached fragments of this distinctive species were found at each of the stations indicated. All were dead and worn, and none gave any indication of what the colony form might have been. It appears to belong to *Chaperia* but, in view of the poor state of the material and the uncertainty regarding the status of at least one South African species of this genus (p. 19), it seems inappropriate to assign a specific name.

Notocoryne Hayward & Cook, 1979

Notocoryne Hayward & Cook, 1979: 54.

Notocoryne cervicornis Hayward & Cook, 1979

Notocoryne cervicornis Hayward & Cook, 1979: 55, fig. 3.

Material

Stations SM 151, SM 163, SM 163/164, SM 180, SM 184, SM 185.

Remarks

The present material shows a greater range of colony size than that originally described by Hayward & Cook (1979), with specimens of 9,5 mm, 10 mm, and 11 mm in length. In all cases the characteristic faceted club-shape was constant. None of the colonies was alive when collected.

Family **Hiantoporidae** MacGillivray, 1895

Hiantoporidae MacGillivray, 1895: 60. Osburn, 1950: 97.

Dactylostega gen. nov.

Colony encrusting, unilaminar, or erect, bilaminar. Cryptocyst developed as a narrow rim; gymnocyst reduced, obscured. Avicularia interzooidal, developed from a series of chambers present between the autozooids; other chambers with simple frontal foramina assumed to be kenozooidal. Secondary calcification originating from interzooidal chambers, projecting over the frontal membrane of the autozooids as a series of blunt, irregular spikes infilling concavities between autozooids and forming an enveloping ooecial cover. Autozooids communicating with interzooidal chambers via small uniporous septula. Ovicell hyperstomial, closed by zooidal operculum. Spines absent.

Type species: *Dactylostega prima* sp. nov.

Etymology

Dactylos (Gr.)—finger; *stegos* (Gr.)—roof, describing the digitate frontal shield seen in later ontogeny.

Dactylostega prima sp. nov.

Figs 7B, 8A

Material

Holotype: SAM–A26416, station SM 185, 33°39,3'S 27°11,6'E, 90 m.

Other material: stations SM 131, SM 162, SM 163, SM 163/164, SM 164, SM 179, SM 180, SM 184, SM 185.

Description

Colony encrusting, unilaminar, or forming erect bilaminar sheets. Zooids oval, deep; boundaries clear at the growing edge of the colony, but obscured by the development of interzooidal avicularia and ?kenozooidal chambers. Opesia oval, rimmed by a narrow, granular, basally deflected cryptocyst with distinct beaded edge; of constant width around whole of opesia. Spaces between zooids infilled by a continuous series of chambers, some of which develop as avicularia, others forming irregular bodies with a frontal foramen (?opesia) surrounded by a granular area of calcification (?cryptocyst). Avicularia most frequently situated distolaterally to zooids, but often lateral in position as well, particularly at the bifurcation of zooid rows. Interzooidal calcification increasing in later ontogeny, appearing continuous over all of the interzooidal chambers and forming a continuous projecting rim around the opesia of each zooid, the edge developing short irregular processes that extend above the frontal membrane. Ovicell immersed, hyperstomial; slightly broader than long with a rather rectangular outline; apparently with a small central ectooecial fenestra in early ontogeny, later covered by calcification derived from the interzooidal chambers

Etymology

Primus (L.)—first, denoting the type species.

Remarks

The overarched 'pericystal' processes seen in *D. prima* produce an effect similar to that of the frontal shield seen in, for example, *Arachnopusia*. However, it may be seen from the micrographs (Fig. 7B) that in *D. prima* this calcification emanated from the curious interzooidal chambers that characterize the genus. The possible homology of the central foramen of the chamber and its surrounding area of granular calcification with the opesia and cryptocyst of the autozooid, and the small uniporous septula that link each chamber with the zooids adjoining it, suggest its kenozooidal nature.

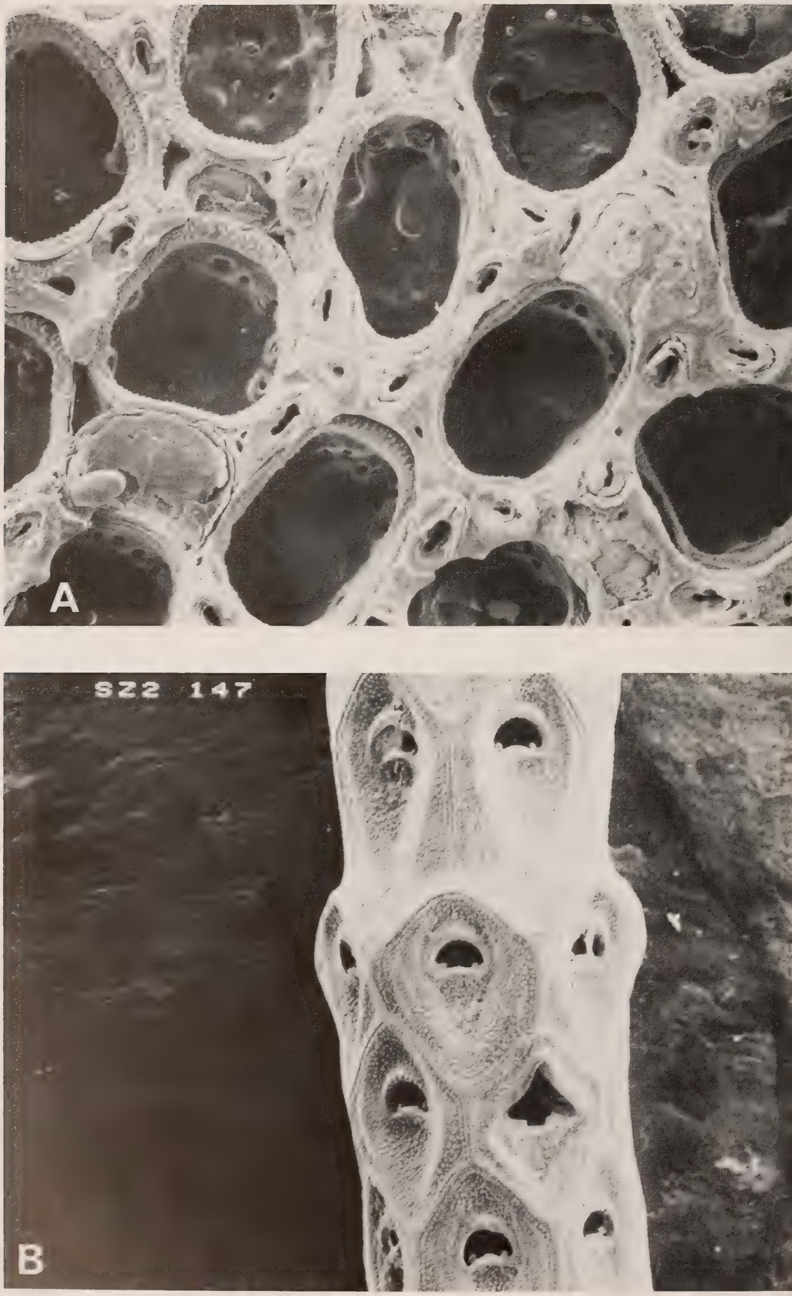

Fig. 8. A. *Dactylostega prima* sp. nov., showing ovicells and kenozooidal chambers in various stages of development. × 50. B. *Cellaria punctata* (Busk). × 80.

Live encrusting colonies were collected from each of the stations listed above, and dead fragments of bilaminar sheets were obtained from SM 180 and SM 164.

Foveolaria tubigera Busk (1884: 68), presently known only from Simon's Bay, Cape of Good Hope, shows many similarities to *D. prima*, in particular the interzooidal chambers, and clearly belongs in the same genus (see fig. 7C). Other species referable to *Dactylostega* are *Hincksina nigrans* (Hincks) (see Osburn 1950: 44, pl. 5 (figs 3–4)) and *Membraniporidra spissimuralis* as described by Hayami (1975: 102, pl. 13 (fig. 10)). Both these forms occur in the Northern Pacific, *D. nigrans* being circumarctic and *D. spissimuralis* Hayami (*non* Canu & Bassler) having been reported from the Pliocene of Japan. A similar development of supraopesial denticulations and frontal avicularia occurs in *Odontionella cyclops* var. *tessellata* (see Brown 1952).

Measurements (means of 25 values) in mm

Lz	lz
0,62	0,42

Family **Arachnopusiidae** Jullien, 1888

Arachnopusiidae Jullien, 1888: 62. Moyano, 1970: 260.

Arachnopusia Jullien, 1888

Arachnopusia Jullien, 1888: 62. Moyano, 1970: 260.

Arachnopusia corniculata sp. nov.

Fig. 9B–C

Material

Holotype: SAM–A26417, station SM 163, 33°04,6′S 28°06,6′E, 90 m.
Other material: stations SM 131, SM 163/164, SM 164, SM 250.

Description

Colony encrusting, unilaminar, zooids oval, separated by shallow grooves, distinct at growing edge, but obscured in later ontogenetic stages. Frontal membrane occupying most of frontal surface; a minimal area of smooth gymnocyst proximally, and a narrow, granular cryptocystal rim, occasionally developing a scalloped edge. Frontal shield developed from the proximal and lateral edges of the zooid as a variable number of processes, fused medially to obscure two-thirds of the total length of the frontal surface, leaving a D-shaped distal aperture and a variable number (typically 3–6) of irregularly shaped foramina. Area of each foramen subsequently reduced by further calcified processes, which may fuse to divide it into two. Proximal border of aperture straight, or developing a short, lobed or multipointed, medial process at an oblique angle to the frontal plane. Similar processes occasionally present on the

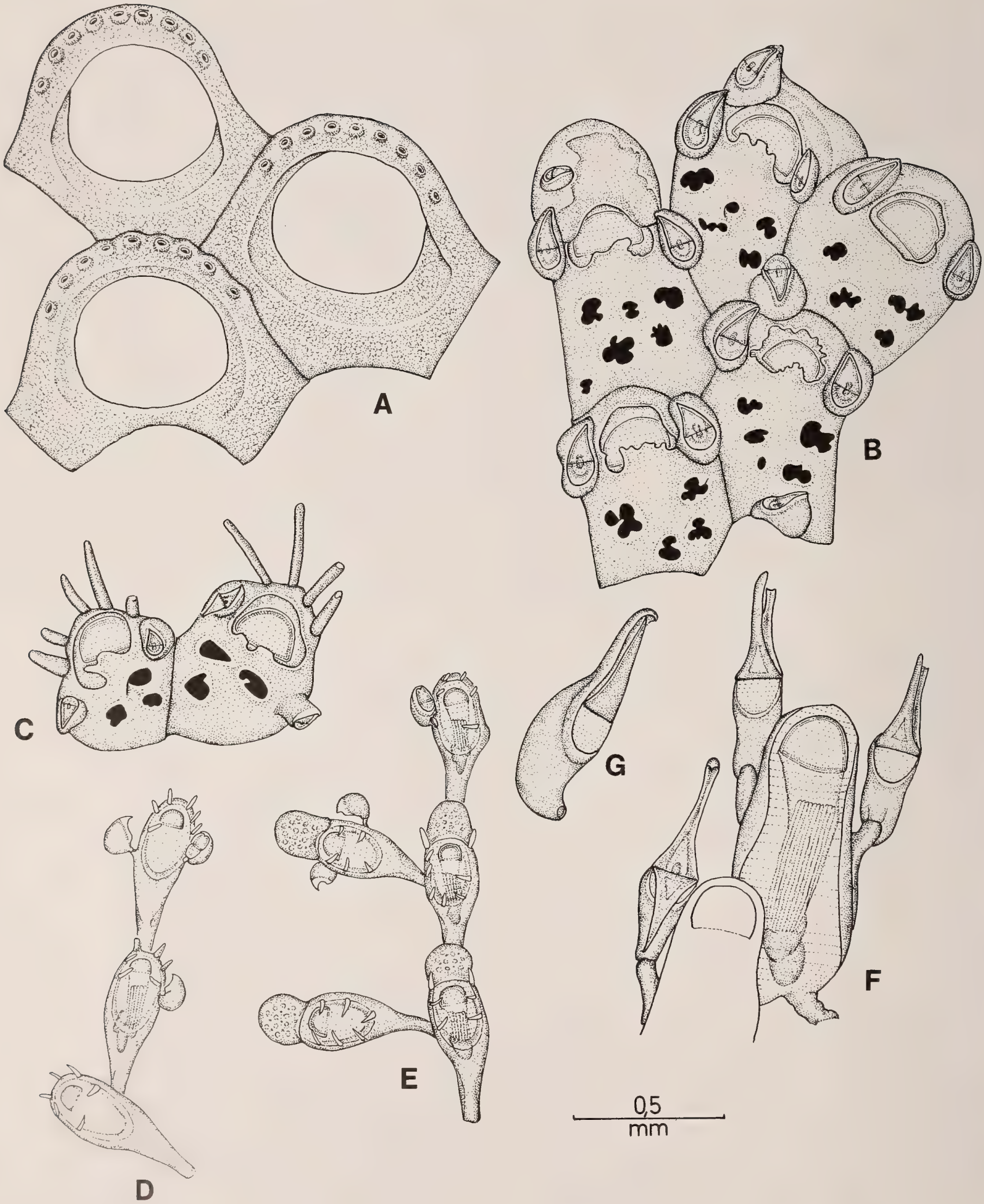

Fig. 9. A. *Chaperia* sp. B–C. *Arachnopusia corniculata* sp. nov. B. Zooids from the growing edge of the colony, including one with an ovicell. C. Two zooids from a juvenile colony showing stages in the development of the frontal shield. D–E. *Bugulella problematica* sp. nov. D. Zooids with distal spines, and avicularia developed from lateral septula. E. Zooids with spines almost encircling the opesiae; avicularia and zooids arising from lateral septula. F–G. *Beania rediviva* sp. nov. F. Showing the rounded distal end of the autozooid. Note that the rostra of the two distal avicularia are broken short. G. An avicularium in lateral view.

distal edge of the aperture; oral spines absent. Avicularia adventitious, typically paired, lateral to aperture; rostrum acute triangular, slightly curved, directed distally or distomedially. Less frequently, avicularia may occur proximally, on the edges of the zooid, with variable orientation. Ovicell hyperstomial, partly immersed, closed by zooidal operculum; as broad as long, smooth and imperforate, becoming obscured by calcification derived from the frontal shield of the distally succeeding zooid. Ancestrula tatiform, 0,4 mm long; opesia oval with a narrow cryptocyst, bordered by spines. First zooids budded from the ancestrula have five long oral spines.

Etymology

Corniculata (L.)—horned, referring to the lip of the aperture.

Remarks

The genus *Arachnopusia* has a wide distribution within the southern hemisphere, although none of the described species has been reported from South Africa. *A. corniculata* may be distinguished readily from other species of the genus by the relatively large, paired, oral avicularia, and in particular the laterally curved rostrum, and by the denticulate proximal border of the aperture. The absence of oral spines is also a distinctive feature.

Measurements (means of 25 values) in mm

Lz	lz
0,64	0,27

Family **Microporidae** Gray, 1848

Microporidae Gray, 1848: 115, 147. Ryland & Hayward, 1977: 112.

Micropora Gray, 1848

Micropora Gray, 1848: 115, 147. Ryland & Hayward, 1977: 112.

Micropora similis sp. nov.

Fig. 5B

Material

Holotype: SAM–A26418, station SM 163, 33°04,6′S 28°06,6′E, 90 m.

Other material: stations SM 163, SM 163/164, SM 164, SM 180, SM 233, SM 239, SM 250.

Description

Colony forming thin unilaminar sheets. Zooids small, broad and flat, hexagonal, or with proximal half distinctly tapered. Opesia (orifice) twice as wide as long, proximal border straight, lateral corners rounded to give a more or less elliptical effect; somewhat more angular in old or ovicellate zooids.

Lateral walls finely crenulate, slightly raised above the frontal surface, forming small scarcely discernible bosses adjacent to the opesia. Cryptocyst finely granular, punctured by numerous small pores; gently convex medially, distally becoming concave close to the opesiules and steeply raised at the proximal edge of the opesia. Opesiules situated close to opesia, distinct. Ovicell recumbent on succeeding zooid, wider than long and rather depressed, with a transverse frontal ridge, frequently developed medially into a low umbo. Avicularia developed sporadically throughout the colony, each situated immediately distal to an autozooid and orientated transverse to distalproximal axis; rostrum semi-elliptical or bluntly triangular, oblique to frontal plane of zooid, cross-bar slender, cylindrical.

Etymology

Similis (L.)—resembling, a reference to the similarity of this species to other members of the genus.

Remarks

This small species resembles the north-eastern Atlantic *Micropora normani* Levinsen, which also possesses interzooidal avicularia. *M. similis* is distinguished from this and other species of the genus, however, by its slender opesia and by the densely punctured frontal wall.

Measurements (means of 15 (zooids) or 10 (avicularia) values) in mm

Lz	lz	Lav
0,54	0,44	0,15

Family **Steginoporellidae** Hincks, 1884, emend. Bassler, 1953

Steganoporellidae Hincks, 1884: 358.
Steginoporellidae: Bassler, 1953: G171.

Steginoporella Smitt, 1873

Steginoporella Smitt, 1873: 15. Pouyet & David, 1979: 764.
Steganoporella: Cook, 1964*a*: 45.

Steginoporella buskii Harmer, 1900

Steganoporella buskii Harmer, 1900: 272, pl. 12 (fig. 13), pl. 13 (figs 33–35). Cook, 1964*a*: 46, pl. 1 (figs 1–3), fig. 1
Steginoporella buskii: Pouyet & David, 1979: 771, pl. 1 (fig. 9), text-fig. 2.

Material

Stations SM 131, SM 163, SM 163/164, SM 164.

Remarks

Fragments of living colonies were collected from stations SM 163/164 and SM 164, but the specimens from SM 131 and SM 163 were of dead, transported

material. The specimens resemble others from Port Elizabeth (the type locality) in having a fairly low level insertion of the cryptocyst in the distal wall (see Cook 1964*a*). Although *S. magnilabris* (Busk) is known from east Africa, all records of it from South Africa are referable to *S. buskii*.

Family **Macroporidae** Uttley, 1949

Macroporidae Uttley, 1949: 175. Brown, 1952: 134.

Macropora MacGillivray, 1895

Macropora MacGillivray, 1895: 54. Brown, 1952: 134.

Macropora africana sp. nov.

Fig. 5C–F

Material

Holotype: SAM–A26419, station SM 163, 33°04,6′S 28°06,6′E, 90 m.
Other material: stations SM 163/164, SM 184, SM 185.

Description

Colony encrusting, unilaminar. Zooids broadly hexagonal, convex, separated by deep grooves. Primary orifice semi-elliptical, proximal border straight, closed by a distinctive calcified operculum with a finely granular, punctate surface. Four or five short, thickened, distal oral spines present but lost in later ontogenetic stages, only the brown chitinized bases remaining. Frontal wall finely granular, perforated by numerous small pores; large dietellae visible at the base of the vertical walls in zooids at the growing edge. Vicarious avicularia sporadically distributed throughout colony, of a primitive form; cystid of similar size to an autozooid, rostrum linguiform with a triangular palatal foramen. Ovicell inflated, large (0,8 mm long), obscuring most of the frontal wall of the succeeding zooid from which it is derived; with a frontal umbo and a series of conspicuous radiating striations and marginal slits, closed by zooidal operculum. Ancestrula similar to later zooids but smaller (0,56 mm long), with seven oral spines.

Etymology

Africanus (L.)—African.

Remarks

Macropora is an ancient genus known mostly from the Tertiary deposits of Australia and New Zealand. The type species, *M. centralis* MacGillivray (Miocene, Victoria), is possibly synonymous with *M. grandis* (Hutton) whose distribution in time extends from the Lower Miocene to the present (Brown 1952). Recent specimens have been reported from New Zealand (Uttley & Bullivant 1972) and the Philippines (Brown 1952). *M. grandis* is a larger species

than *M. africana*, with zooids up to 1,2 mm long, and is further distinguished by a proportionally more elongate operculum and distinct oral shelf, by the possession of a distinct raised peristome, by a complete absence of oral spines, and by the absence of a zooid orifice distal to the ovicell.

Measurements (means of 25 values) in mm

Lz	lz
0,78	0,62

Family **Cellariidae** Hincks, 1880

Cellariidae Hincks, 1880: 103. Ryland & Hayward, 1977: 119.

Cellaria Ellis & Solander, 1786

Cellaria Ellis & Solander, 1786: 18. Ryland & Hayward, 1977: 119.

Cellaria tectiformis Hayward & Cook, 1979

Cellaria tectiformis Hayward & Cook, 1979: 69, fig. 7.

Material

Stations SM 103, SM 131, SM 151, SM 233, SM 234.

Remarks

A single large, living, colony was obtained from each of the two stations SM 233, and SM 234.

Cellaria punctata (Busk, 1852)

Fig. 8B

Salicornaria punctata Busk, 1852: 366 (*partim*).
Cellaria gracilis: Marcus, 1922: 19, fig. 11.
Cellaria punctata: Harmer, 1926: 337, pl. 21 (figs 14–16), text-fig. 13a.

Material

Stations SM 163/164, SM 164, SM 180.

Description

Colony forming diffuse, straggling tufts up to 50 mm high. Joints consisting of tangled masses of brown, chitinous tubes, each arising from inconspicuous calcified sockets on the frontal surfaces of the zooids at the distal and proximal end of each internode, possibly representing kenozooids. Internodes straight or gently curved, up to 8 mm long, with a maximum width of 0,7 mm, typically broadening distally, with distinct dilatations along length; comprised of five to seven longitudinal series of zooids. Autozooids regularly

hexagonal, separated by distinct sutures; cryptocyst granular, concave, the central area particularly depressed and delimited by a prominent ridge. Opesia situated in distal third of zooid, semicircular; distal border raised, forming a distinct cowl, with finely beaded edge; proximal border with a projecting, rounded lip, and a pair of thick lateral denticles. Avicularia vicarious, infrequent, typically present at distal end of each internode, close to joint; as large as autozooid, with a broadly triangular rostrum occupying half frontal surface, supporting a distally directed triangular mandible. Proximal border of avicularian opesia with an anvil-shaped lip, distal corners of which fuse with sides of opesia to delimit paired lateral opesiules; palate scarcely developed, with a large rounded foramen. Fertile zooids constitute the characteristic dilatations, typically seven in a whorl; ovicellar orifice inconspicuous, largely occluded by a proximal projection from the succeeding zooid.

Remarks

This species was described by Busk (1852) from Queensland and redescribed by Harmer (1926), who examined material from a number of Indo-Pacific localities and included Marcus's (1922) South African specimens and Thornley's (1905, given as 1895 in error) Ceylon material of '*Cellaria johnsoni*' in his synonymy. The present material shows some differences from the specimens studied by Harmer (for example, Holborn Island, Queensland, BMNH 1928.9.13.87), most notably in zooid numbers. In the Holborn Island specimen each internode comprises four to six longitudinal series of zooids; in the *Meiring Naude* material the proximal end of each internode has five series of zooids, broadens rapidly to six, and has seven in the fertile swellings. The avicularian rostrum is more rounded in the Australian material, but zooid morphology and size are comparable with the South African specimens. A specimen from the Red Sea (BMNH 1963.8.10.37 pt.) is identical to the *Meiring Naude* specimens.

Measurements (means of 25 values) in mm

Lz	lz
0,48	0,29

Cellaria paradoxa Hayward & Cook, 1979

Cellaria paradoxa Hayward & Cook, 1979: 71, fig. 8.

Material

Station SM 103.

Remarks

Worn internodes of this species were present in the coarser sediment fraction from station SM 103. A somewhat similar species with dimorphic

zooids was described from the Eocene of North and South Carolina as *C. bifaciata* by Canu & Bassler (1920: 274, pl. 40 (figs 14–17)).

Family **Aspidostomatidae** Jullien, 1888

Aspidostomatidae Jullien, 1888: 77. Harmer, 1926: 322.

Aspidostoma Hincks, 1881

Aspidostoma Hincks, 1881: 159. Harmer, 1926: 323.

Aspidostoma livida sp. nov.

Fig. 10

Material

Holotype: SAM–A26420, station SM 239, 32°14,8′S 29°00,8′E, 90 m.
Other material: stations SM 131, SM 164, SM 184, SM 239.

Description

Colony erect, bilaminar, reticulate, forming broad, plate-like lobes, largest fragment obtained measuring 45×50 mm; alcohol-preserved material retaining a deep blue-grey colour. Fenestrulae up to 4 mm long, apparently regularly distributed, about four occurring in each cm^2 of colony surface. Zooids hexagonal, convex, separated by distinct grooves, thickly calcified with a coarsely granular surface. Frontal wall convex proximally, dipping distally towards a small deep-set opesia; proximal edge of opesia (delimiting the 'polypide tube') forming a thickened axehead-shaped lip. A thick median ridge extends for a short distance proximally from the outer edge of the opesial lip. Distal end of zooid raised as a prominent hood, frequently developed on each corner into short flattened processes. Operculum transversely oval, thickly calcified, white. Ovicell globose, rather flattened frontally, with a coarsely granular surface; opening via a hooded aperture distal to the zooid operculum. Interzooidal avicularia sporadically distributed over the colony; rostrum acute triangular, distolaterally directed; cross-bar incomplete, palate with an elliptical central foramen. Fenestrulae rimmed by single series of large kenozooids.

Groups of frontally budded zooids appear to inaugurate new laminae. The form of the colony could not be discerned, but the large bilaminar plates were flat or gently dished, rather than convoluted, and new plates appear to develop perpendicular to their predecessors. Unlike the fenestrate colonies of *Dimorphocella moderna* (see p. 48) from the same station, *A. livida* shows no formation of central ribs of calcification.

Etymology

Lividus (L.)—bluish, referring to the colour of the colony.

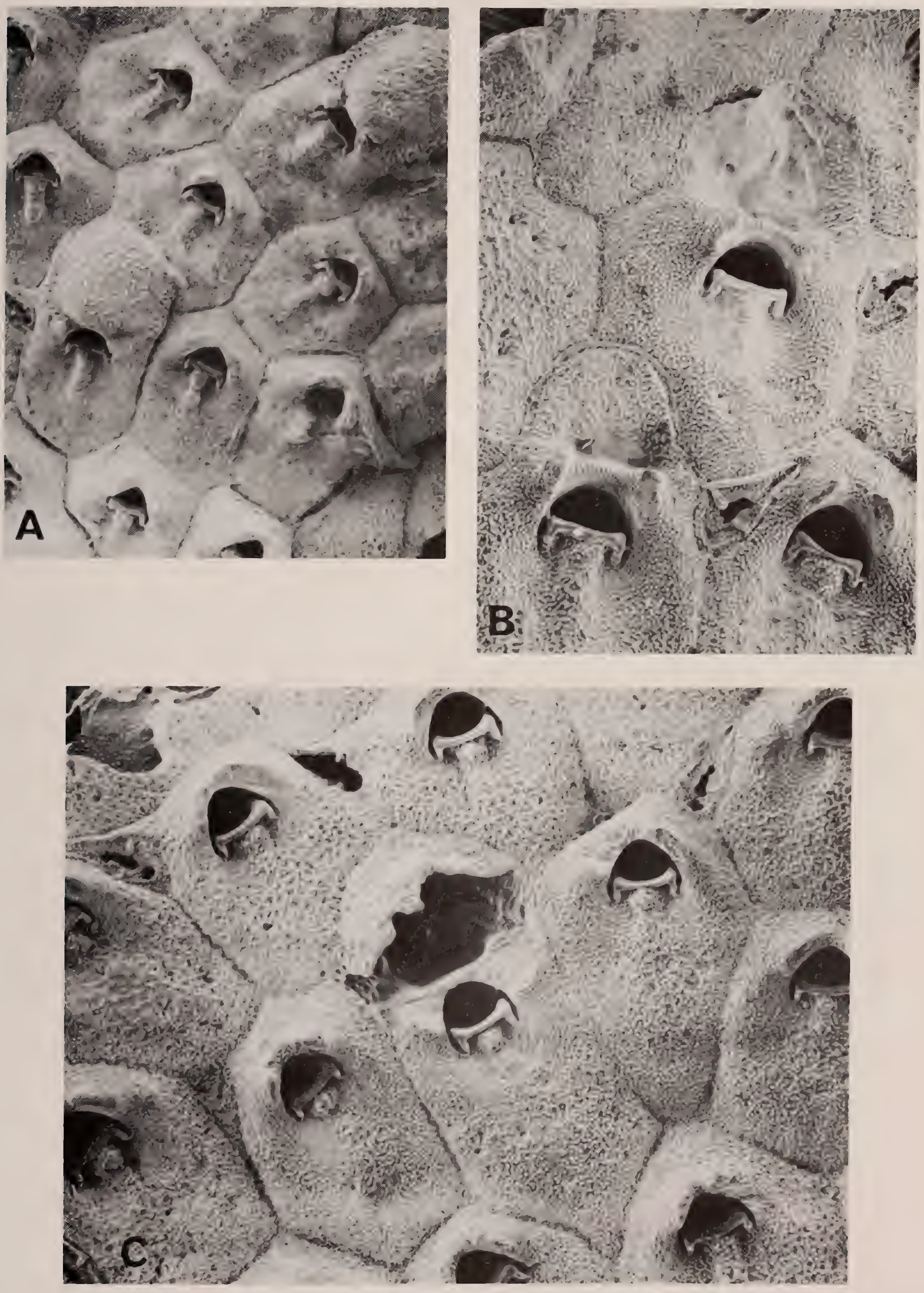

Fig. 10. *Aspidostoma livida* sp. nov. A. Portion of a colony, including two ovicelled zooids and (bottom right) two kenozooids. × 25. B. Developing ovicells, and avicularia. × 40. C. Detail of a damaged ovicell. × 40.

Remarks

The material from station SM 239 comprised a large number of reticulate fragments which may have represented just one large colony, no basal attachment was found. The only erect Recent species of *Aspidostoma* develop slender cylindrical colonies, although Waters (1905: 243) described specimens of *A. giganteum* (Busk) that displayed a loosely anastomosing form. Erect branched species of *Aspidostoma* were described from the Tertiary of New Zealand by Brown (1952).

Measurements (means of 25 values) in mm

Lz	lz
0,89	0,73

Family **Scrupocellariidae** Levinsen, 1909

Scrupocellariidae Levinsen, 1909: 130. Ryland & Hayward, 1977: 128.

Caberea Lamouroux, 1816

Caberea Lamouroux, 1816: 128. Ryland & Hayward, 1977: 128.

Caberea darwinii Busk, 1884

Caberea darwinii Busk, 1884: 29, pl. 32 (fig. 6c–f).
Caberea darwinii: Hastings, 1943: 374, pl. 5 (figs 1–3), text-figs 21, 22A–C, 23A–D, 24A.

Material

Stations SM 163/164, SM 179, SM 184, SM 185, SM 239.

Remarks

The geographical distribution of *Caberea darwinii* has been discussed at length by Hastings (1943). It extends from New Zealand westward to the Patagonian Shelf and is widespread in Antarctic and Subantarctic waters; it has been recorded from Kerguelen, Prince Edward Island, and Marion Island, but has not been reported before from South Africa.

Eupaxia Hasenbank, 1932

Eupaxia Hasenbank, 1932: 321, 363.

Eupaxia quadrata (Busk, 1884)

Cellularia quadrata Busk, 1884: 18, pl. 5 (fig. 5).
Eupaxia incarnata Hasenbank, 1932: 363, fig. 30A–C.
Eupaxia quadrata: Hayward & Cook, 1979: 63, fig. 6C–F.

Material

Station SM 232.

Remarks

This species was redescribed and figured by Hayward & Cook (1979). A single fragment of a live colony was collected during the present survey.

Menipea Lamouroux, 1812

Menipea Lamouroux, 1812: 183. Harmer, 1923: 339. Hastings, 1943: 331.

Menipea crispa (Pallas, 1766)

Cellularia crispa Pallas, 1766: 71.
Menipea crispa: Marcus, 1922: 11. Hastings, 1943: 332. O'Donoghue, 1957: 75, figs 1–2.

Material

Stations SM 163/164, SM 164, SM 179.

Remarks

M. crispa appears to have a limited geographical distribution, from Saldanha Bay (South Africa) to Madagascar (Hastings 1943). Live specimens were collected from each of the three *Meiring Naude* stations, which ranged in depth from 50 to 90 m.

Menipea triseriata Busk, 1852

Menipea triseriata Busk, 1852: 22, pl. 23 (figs 2–4).
Menipea triseriata: Harmer, 1923: 342, pl. 17 (fig. 18), pl. 19 (figs 40–42). O'Donoghue, 1957: 76.

Material

Stations SM 163, SM 164, SM 179, SM 180, SM 185.

Remarks

This distinctive species is known only from South Africa. The present material includes several very large, luxuriantly branched colonies.

Menipea ornata (Busk, 1852)

Cellularia ornata Busk, 1852: 20, pl. 20 (figs 3–4).
Menipea ornata: Harmer, 1923: 340.
Menipea flabellum: Marcus, 1922: 13, fig. 7.
Cellularia infantae O'Donoghue, 1924: 30, pl. 1 (fig. 6). O'Donoghue & De Watteville, 1935: 207; 1937: 12.

Material

Station SM 185.

Remarks

The confused synonymy of this species has been clarified by Harmer (1923) and by Hastings (1943: 332).

Menipea marionensis Busk, 1884

Menipea marionensis Busk, 1884: 21, pl. 4 (figs 3, 3a).
Menipea marionensis: Harmer, 1923: 341, pl. 17 (fig. 22), pl. 19 (figs 43–45).

Material

Stations SM 179, SM 180, SM 185.

Remarks

This species appears to be known only from the Cape of Good Hope. The present specimens were obtained living, at depths of 80 and 90 m.

Family **Bicellariellidae** Levinsen, 1909

Bicellariellidae Levinsen, 1909: 93. Ryland & Hayward, 1977: 146.

Bugulella Verrill, 1879

Bugulella Verrill, 1879: 472. Maturo & Schopf, 1968: 36.

Bugulella australis Hayward & Cook, 1979

Bugulella australis Hayward & Cook, 1979: 64, fig. 6A–B. Millard, 1980: 143.

Material

Station SM 233.

Remarks

The material comprised a tangled mass, probably representing several colonies, and was living when collected. Following its recent description in the first report of the *Meiring Naude* Bryozoa (Hayward & Cook 1979), substantial material was found in the *Galathea* deep-sea collections from a station in the Tasman Sea at 610 m (Hayward 1981).

Measurements (means of 20 values) in mm

Lz	Lop	lop
0,74	0,28	0,18

Bugulella problematica sp. nov.

Fig. 9D–E

Material

Holotype: SAM–A26421, station SM 233, 32°15,2′S 29°09,8′E, 540–580 m.

Description

Colony erect, straggling, delicate; composed of branching uniserial chains of zooids forming a dense tangled tuft. Zooids elongate, club-shaped: oval distally, tapered proximally to a slender tubaeform shape; thinly calcified and

translucent. Opesia oval, with a narrow cryptocyst border; typically with three pairs of slender spines regularly spaced around distal end, rarely up to ten spines distributed around whole of opesial border. Each zooid budding up to three new zooids: one distal, one on each side from a point level with the proximal half of the opesia. Distal bud constant, colony developing as a uniserial chain, some or all of whose members produce secondary chains, on one or both sides, perpendicular to the first; tertiary chains may form in the same way. The lateral budding points, marked by large, distinct septula, may instead give rise to irregularly tubular kenozooids that link with septula of zooids in neighbouring branches; rarely, such kenozooids develop at the distal budding point. Avicularia pedunculate, with short, semi-elliptical mandibles; single, more usually paired, arising from lateral budding points and thus precluding development of side chains where they occur. Rarely, a single avicularium develops distally, frontal to the proximal tubular portion of the next zooid. Ovicell prominent, terminal; spherical, with finely tessellated surface, closed by zooidal operculum.

Etymology

Problematicos (Gr.)—problematical.

Remarks

The budding pattern of *Bugulella problematica*, and the paired lateral avicularia, serve to distinguish it from *B. australis* (above), in which lateral branches are initiated by a second distal bud, which becomes fused with a tubular structure (?kenozooid) arising from the lateral septulum of its twin. The avicularium of *B. australis* is constantly distal in position, and the zooids tend to be larger than those of *B. problematica*. However, zooids of the latter species may be found with up to ten opesial spines, typical of *B. australis*, and the ovicell is practically identical in both species. Specimens of the two species were found intermingled in the same sample and some doubt must remain that the apparently significant difference in budding pattern may prove to be an astogenetic effect.

Measurements (means of 20 values) in mm

Lz	Lop	lop
0,51	0,25	0,15

Family **Beaniidae** Canu & Bassler, 1927

Beaniidae Canu & Bassler, 1927: 14. Ryland & Hayward, 1977: 150.

Beania Johnston, 1840

Beania Johnston, 1840: 272. Ryland & Hayward, 1977: 150.

Beania magellanica (Busk, 1852)

Diachoris magellanica Busk, 1852: 54, pl. 67 (figs 1–3).
Beania magellanica: Hastings, 1943: 414, figs 34C, 35G.

Material

Stations SM 163, SM 179, SM 239.

Distribution

Widespread; reported from the Mediterranean to the Falkland Islands, from Australia to Japan, and throughout the Indian Ocean. Recorded from South Africa by Marcus (1922) and O'Donoghue (1957).

Beania rediviva sp. nov.

Fig. 9F–G

Beania erecta: Hasenbank, 1932: 342, fig. 15A–C.

Material

Holotype: SAM–A26422, station SM 250, 31°59,3′S 29°22,5′E, 150–200 m.

Etymology

Redivivus (L.)—renewed, alluding to the newly recognized identity of the species.

Remarks

The Antarctic–Subantarctic *Beania erecta* Waters was redescribed by Hastings (1943: 416), who excluded Hasenbank's (1932) record from Agulhas Bank from her synonymy. Hasenbank's figure showed several significant differences from typical *B. erecta*: the distal ends of the zooids were smoothly rounded, lacking the paired lateral oral projections seen in *B. erecta*, and the avicularia were very large, with a slender, strongly hooked rostrum comprising almost half the total length. These features are shown particularly well in the present specimen (Fig. 9G) and it is appropriate to introduce a new name for Hasenbank's species.

Family **Bugulidae** Gray, 1848

Bugulidae Gray, 1848: 110, 146. Ryland & Hayward, 1977: 151.

Bugula Oken, 1815

Bugula Oken, 1815: 89. Ryland & Hayward, 1977: 151.

Bugula dentata (Lamouroux, 1816)

Acamarchis dentata Lamouroux, 1816: 135, pl. 3 (fig. 3a–b).
Bugula dentata: O'Donoghue, 1924: 33; 1957: 82. Harmer, 1926: 439, pl. 30 (figs 5–6), pl. 32 (figs 21–25).

Material

Station SM 180.

Remarks

This well-characterized species was reported from South Africa by O'Donoghue (1924), who collected it on the lower shore at Agulhas Light, Cape Province. All South African records were documented in a later paper (O'Donoghue 1957).

Family **Cribrilinidae** Hincks, 1880

Cribrilinidae Hincks, 1880: 182. Hayward & Ryland, 1979: 56.

Cribrilaria Canu & Bassler, 1929

Cribrilaria Canu & Bassler, 1929: 33. Hayward & Ryland, 1979: 62.

Cribrilaria innominata (Couch, 1844)

Lepralia innominata Couch, 1844: 114, pl. 22 (fig. 4).
Cribrilaria innominata: Harmelin, 1970: 84, figs 1d–f, 2, pl. 1 (figs 4–6). Hayward & Ryland, 1979: 64, fig. 17.

Material

Stations SM 163, SM 163/164.

Remarks

This widespread species is characterized by its umbonate frontal shield, and the presence of a large, conspicuous, suboral lacuna. Live colonies were collected at both of the above stations.

Cribrilaria venusta (Canu & Bassler, 1925)

Fig. 11A

Puellina venusta Canu & Bassler, 1925: 22, pl. 2 (fig. 5).
Cribrilaria venusta: Harmelin, 1976*a*: 180, pl. 2 (figs 3–5).

Material

Station SM 239.

Remarks

This is a distinctive species recognized initially by its broad and relatively flat frontal shield composed of numerous slender costae. These are usually little thickened, though occasionally developing a series of peripheral knobs. The first pair of costae proximal to the orifice fuse and thicken medially to form a triangular umbo and there are no suboral pores; conversely the pores between the umbonate first pair of costae and the second pair are typically large and distinct. There are five oral spines. The avicularian rostrum is slender, acuminate, and frequently with a gentle lateral curve.

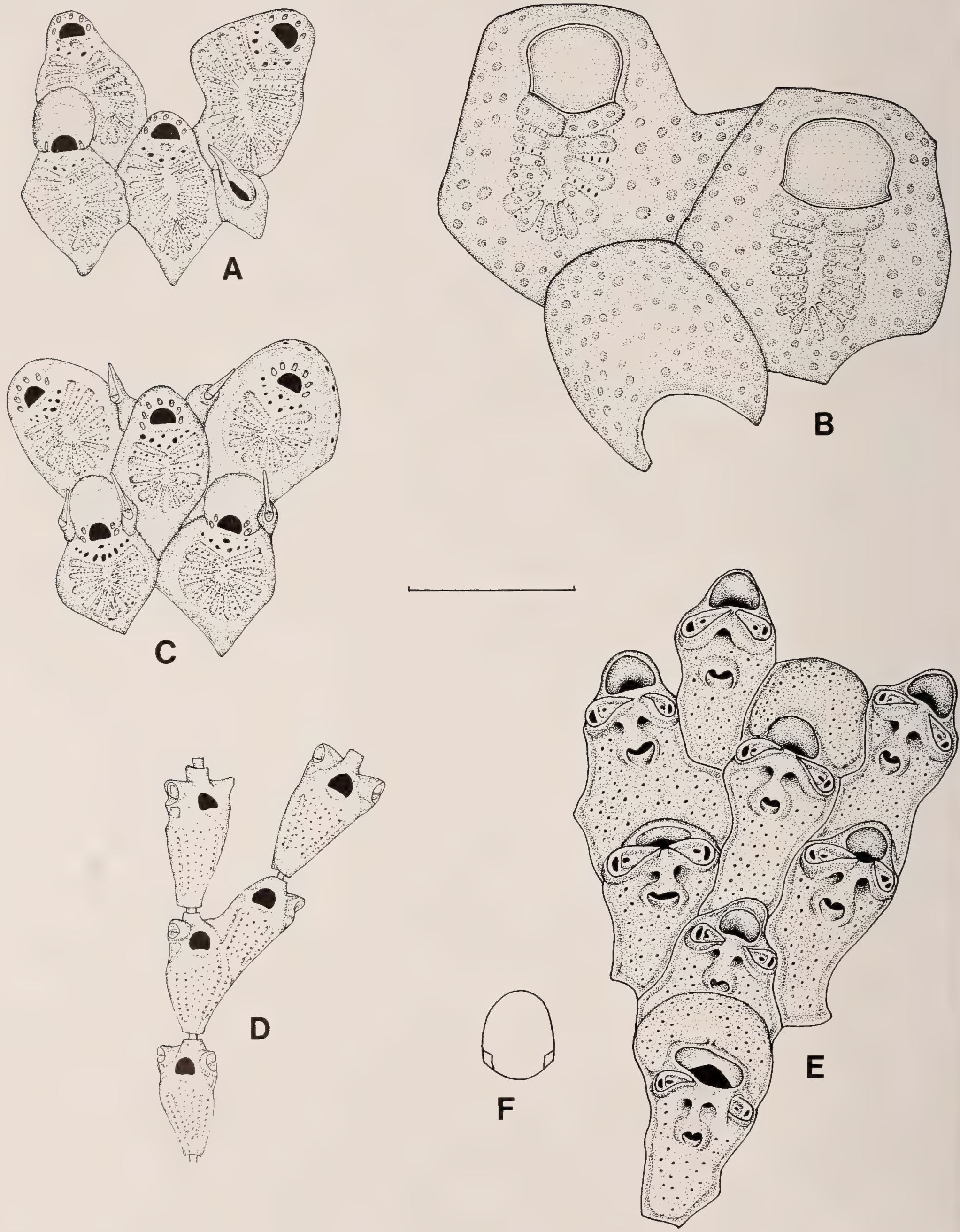

Fig. 11. A. *Cribrilaria venusta* (Canu & Bassler). B. *Figularia* sp., two zooids, with an ovicell from a missing zooid. C. *Cribrilaria africana* sp. nov., a specimen from SM 164. D. *Vittaticella* sp. E–F. *Gigantopora foraminosa* sp. nov. E. Portion of a branch, showing progressive elaboration of the spiramen. F. Outline diagram of primary orifice. Scale = 0,5 mm for A–D, F; 1 mm for E.

Cribrilaria venusta has only recently been redescribed by Harmelin (1976*a*), who summarized its known distribution. The present material is closely similar in zooid size (0,46–0,6 mm × 0,38–0,44 mm) and morphology to specimens collected from the western end of the English Channel. Although the present record marks a significant extension of its geographical range, the distribution of *C. venusta*, like those of other species of *Cribrilaria*, is imperfectly known and will probably prove to be very broad.

Cribrilaria africana sp. nov.

Fig. 11C

Material

Holotype: SAM–A26423, station SM 164, 33°04,6′S 28°06,6′E, 90 m.
Other material: stations SM 163, SM 250.

Description

Colony encrusting. Zooids oval, rather flat; costate frontal shield comprising larger part of frontal surface, with only a narrow rim of gymnocyst. Costae with small marginal tubercles, but without a central umbo. Orifice with straight, smooth proximal edge, six or seven closely spaced oral spines. Suboral region (between orificial bar and first pair of frontal costae) broad, triangular and flat, with up to five large pores, and many small pores. Avicularium small, squeezed in between successive zooids, or occasionally developed on gymnocyst, semi-pedunculate; rostrum slender, *c*.0,1 mm long. Ovicell small, spherical, hyaline, with a small, median umbo, frequently with an avicularium closely adjacent to it on each side.

Etymology

Africanus (L.)—African.

Remarks

This species is readily distinguishable from those reviewed by Harmelin (1976*a*) by the conspicuous suboral pores and the small semi-pedunculate avicularium.

Measurements (means of 16 values) in mm

Lz	lz
0,39	0,29

Figularia Jullien, 1886

Figularia Jullien, 1886: 608. Hayward & Ryland, 1979: 70.

Figularia philomela (Busk, 1884)

Cribrilina philomela Busk, 1884: 132, pl. 17 (fig. 6).
Figularia philomela: Hayward & Cook, 1979: 76, fig. 9B.

Material

Station SM 163.

Remarks

The present material, comprising several small encrusting live colonies, was collected in waters far shallower than those sampled by the first series of *Meiring Naude* stations.

Figularia sp.

Fig. 11B

Material

Station SM 163.

Remarks

The material comprised two fragments of live colonies, the largest including five complete zooids, together with portions of four others. The zooids were large and flat (0,8–0,9 mm × 0,7–0,8 mm); the costate frontal shield was small, constituting less than half of the total frontal surface, although costae and intercostal pores were distinct. Two or more large pseudopores were present on each of the costae, and the rest of the frontal surface, and the surface of the ovicell, were covered with similar pseudopores, indicated by brown chitinized cuticle. This species does not seem to have been described before, but the paucity of material precludes a complete description being presented here.

Family **Exochellidae** Bassler, 1953

Exochellidae Bassler, 1953: G205. Hayward & Ryland, 1979: 78.

Escharoides Milne Edwards, 1836

Escharoides Milne Edwards, 1836: 218. Hayward & Ryland, 1979: 78.

Escharoides contorta (Busk, 1854)

Eschara contorta Busk, 1854: 89, pl. 108 (figs 1–3).
Mucronella contorta: Busk, 1884: 155, pl. 20 (fig. 9). O'Donoghue & De Watteville, 1937: 18.
Escharoides contorta: O'Donoghue, 1957: 88, figs 10–11.

Material

Stations SM 151, SM 162, SM 163, SM 163/164, SM 164, SM 180, SM 184, SM 185, SM 239.

Remarks

This species is known only from South Africa. It was particularly abundant in the present collections and live colonies were collected from most of the stations listed. Colony form varied greatly, from simple encrusting sheets to broad bilaminar plates and slender, branching cylindrical growths.

Family **Adeonidae** Jullien, 1903

Adeonidae Jullien *in* Jullien & Calvet, 1903: 53. Cook, 1973: 246.

Dimorphocella Maplestone, 1903

Dimorphocella Maplestone, 1903: 140.

Description

Colony erect, branching, bilaminar. Autozooids with sinuate secondary calcified orifice. Frontal shields umbonuloid, zooids surrounded by marginal frontal septula. Brooding zooids dimorphic, large, with wide, non-sinuate orifices; frontal shields with several spiramina. Adventitious avicularia unilateral or paired, acute; interzooidal marginal avicularia sometimes present, mandibles slung on paired condyles.

Remarks

The genus is inferred to have umbonuloid ontogeny of zooid frontal shields, as in *Adeona* and *Adeonellopsis* (see Cook 1973). The enlarged brooding zooids and condylate avicularia are also characteristic of the family. *Dimorphocella* differs from the other genera in the strongly sinuate autozooid orifice, and the apparent lack of frontal spiramen pores in autozooids.

Dimorphocella is known from the Tertiary of Australia, but has not been reported as Recent (see below). The genus was introduced somewhat informally by Maplestone (1903), who stated, 'I propose this genus for a form presently to be described, and *Adeonella triton* McG'. The species then described, *D. pyriformis* Maplestone (1903: 141, pl. 16 (fig. 1)), was illustrated with strongly sinuate autozooid orifices, and paired, medially orientated avicularia. The brooding zooids had an enlarged distal cavity and a central, circular, porous frontal area, and paired avicularia orientated distally. *Adeonella triton* MacGillivray (1895: 90, pl. 19 (fig. 23)) was originally described with similar characters, except that the autozooidal avicularia were unilateral and the brooding zooids were not distally expanded. *A. triton*, as later described by Maplestone (1903, pl. 16 (fig. 2)) had paired, distally orientated avicularia and a denticulate process on the proximal side of the brooding zooid orifice, but appears to be the same species. Although Canu & Bassler (1920: 571, fig. 170A–B; 1929: 384) indicated *A. triton* as 'genotype' of *Dimorphocella*, Maplestone's (1903) choice was definite, if unorthodox, and *D. pyriformis* was later listed as type species by Bassler (1935: 95; 1953: G213, fig. 161, 5). Canu & Bassler (1920) included *Dimorphocella portmarina*

Maplestone (1913: 359, pl. 28 (fig. 5)), a Recent Australian species, in *Dimorphocella*, but this form has conspicuous autozooidal spiramina and is referable to *Adeona* (see Canu & Bassler 1929).

Waters (1881: 340, pl. 18 (fig. 85)), described another Tertiary Australian species as *Schizoporella submersa*. No brooding zooids were described and none have been found in specimens in the British Museum (Natural History) collections (D32901–2, D34733, see fig. 14A). The autozooidal characters of *S. submersa* are similar to those of *D. pyriformis*. *S. submersa* as described by MacGillivray (1895: 82, pl. 11 (figs 8–9)) may not be the same species (see Brown 1958: 60).

Dimorphocella moderna sp. nov.

Figs 12–13

Material

Holotype: SAM–A26424, station SM 239, 32°14,8′S 29°00,8′E, 90 m.
Other material: stations SM 164, SM 179, SM 180, SM 185, SM 250.

Description

Colony erect, bilaminar, fenestrate, deeply pigmented, formed of slightly curved, frequently anastomosing plates. Central part of plates becoming thickened and forming branched strengthening ribs. Zooids arranged in alternate bifurcating and recombining series, forming fenestrulae that are bordered by large interzooidal avicularia. Autozooids with a complete series of marginal frontal septula, sometimes with additional frontal septula. Frontal shields otherwise imperforate except for a suboral spiramen which is occluded early in ontogeny. Secondary calcified orifice with a deep proximal sinus. Brooding zooids very large, raised distally, with a wide orifice, denticulate proximally. Central frontal area with several spiramen pores. Adventitious avicularia usually unilateral, occasionally absent in autozooids, in all cases orientated distally. Large, interzooidal fenestral avicularia acute, with raised rostra, mandibles hinged on prominent paired condyles, orientated distally.

Etymology

Modernus (L.)—of the present, referring to the Recent occurrence of the species.

Remarks

D. moderna is represented by worn fragments from all the stations listed, except from SM 239. This station provided abundant material that was alive when collected. Although no complete colony is present, and the substratum and mode of attachment is unknown, the larger plates indicate that colonies probably exceed 100 mm in height or diameter. Each plate is slightly curved, and the zooids on the outward-facing convex side are occluded by extrazooidal

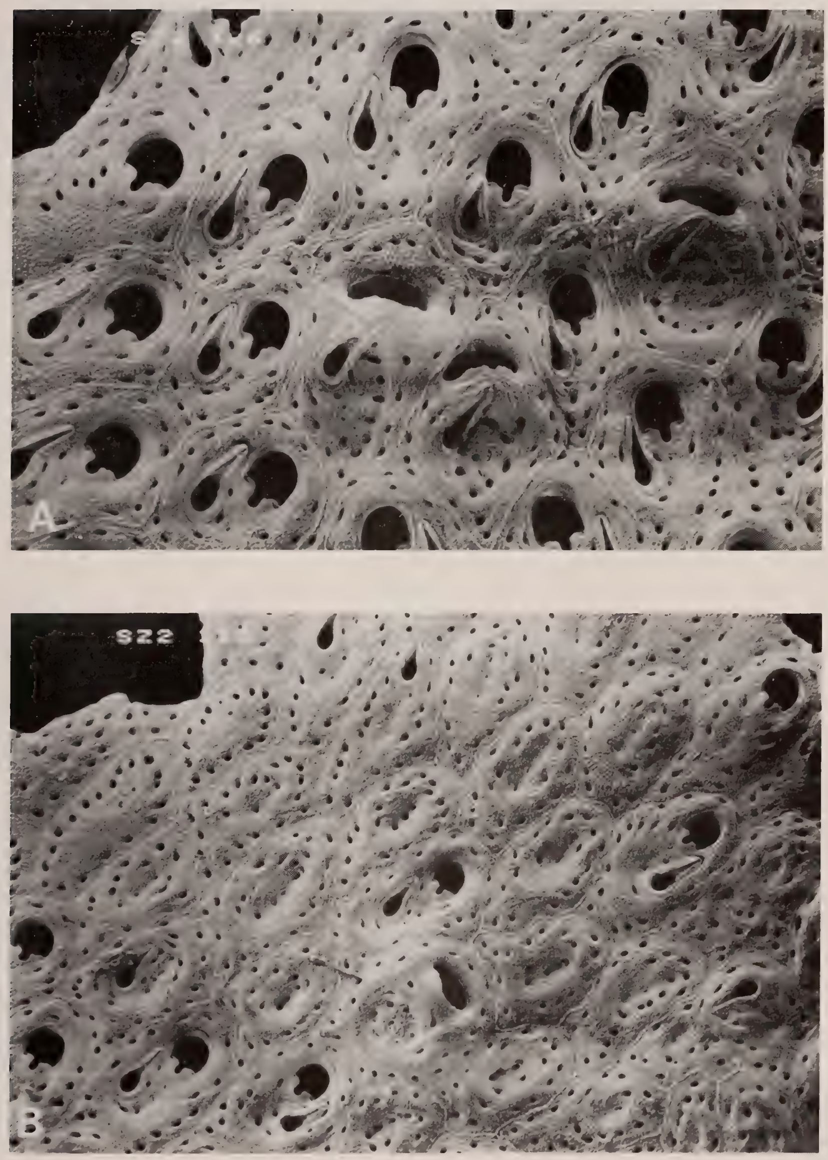

Fig. 12. *Dimorphocella moderna* sp. nov. A. Frontal surface of a branch, showing dimorphic orifices. × 48. B. Basal surface. × 36.

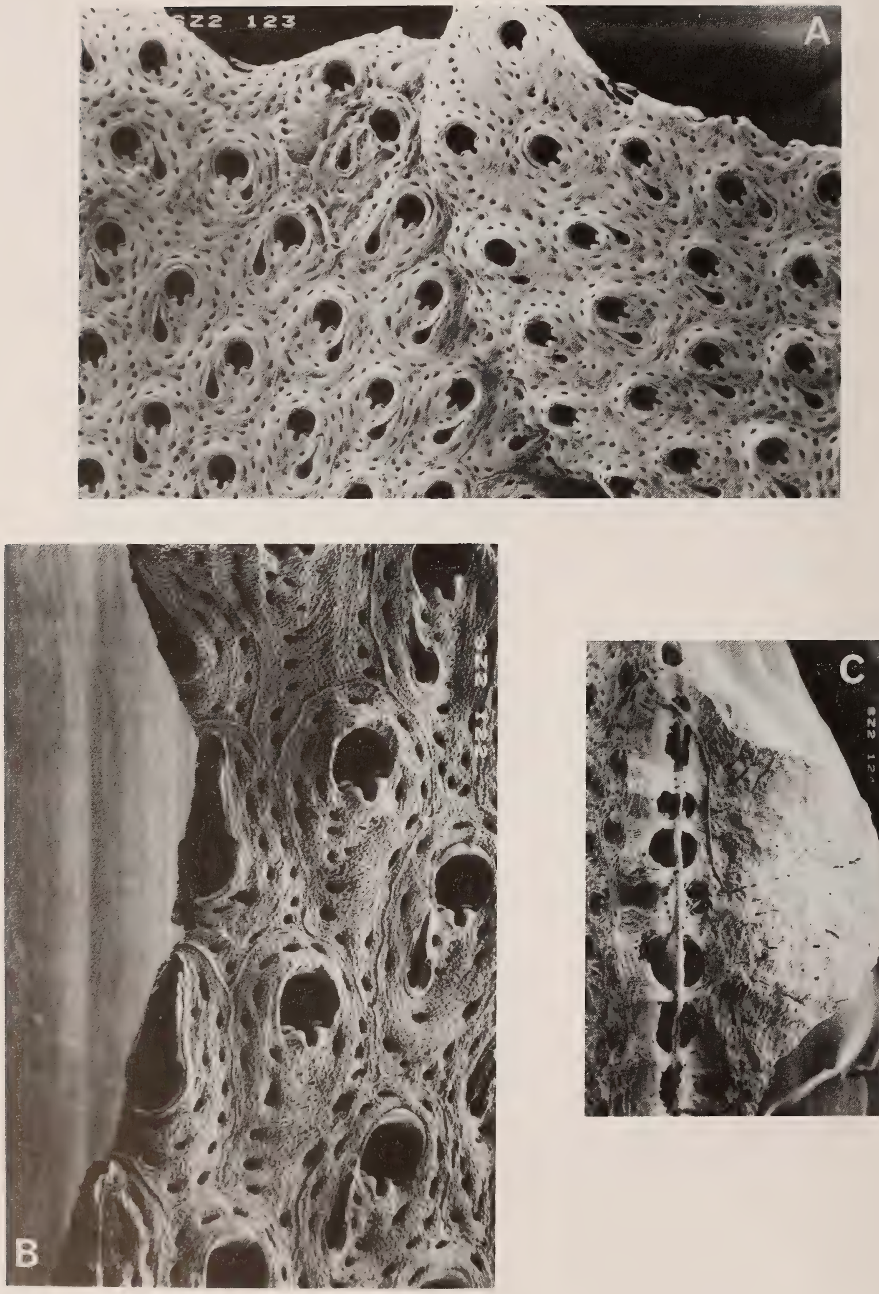

Fig. 13. *Dimorphocella moderna* sp. nov. A. Detail showing fusion of two branches. × 27. B. Margin of a branch with vicarious avicularia. × 66. C. Section of a branch showing frontal thickening. × 24,5.

calcification earlier in astogeny than those of the concave surface (see Fig. 12A–B). Although the budding pattern of plates is primarily in one plane, secondary plates arise later in astogeny at right angles to the primary plates, and anastomose with them. These secondary plates originate from a frontally budded group of three to seven zooids that later form a bilaminar expansion. The central rib of each plate is formed by localized thickening of the frontal shields of zooids, which becomes extrazooidal. The thickening also occurs on the convex surface in advance of that on the concave surface (Fig. 13C), but at the base of the colony is equally developed on both surfaces, forming a cylinder 6 mm in diameter. The frontal shields may exceed 2,80 mm in thickness, but the zooidal cavity is not occluded. Neighbouring unthickened zooids, even at the base of the colony, possess lophophores, and are inferred to have been capable of feeding. The fenestrulae are oval and are formed by the regular bifurcation and recombination of zooid series. They are more frequent in occurrence than those of *Aspidostoma livida* (see p. 36). Some growing edges that had been damaged before collection show that regenerated zooids (with lighter pigmentation) re-form fenestrulae in the same position as before. There is some variation in orifice width among autozooids (see Fig. 13A). This appears to be related to the bifurcation and recombination of series, but by analogy with *Adeonella* (see Harmer 1957), may also reflect a sexual function.

The umbonuloid nature of the frontal calcified shield may be seen at the growing tip of a few young secondary branches of anastomosing plates, which have been protected. The exposed growing edges of the primary plates have been damaged. The minute frontal spiramen is apparently occluded early in ontogeny. This may be correlated with the presence of a sinus in the secondary calcified orifice. This, by analogy with similar sinuate cryptocystidean forms (e.g. *Laminopora*), would allow passage of water into the ascus during protrusion of the lophophore.

Colonies are the substratum for several encrusting bryozoans, cirripedes, foraminifera, serpulids, etc., and have numerous small ophiuroids in the cavities formed by the anastomoses of plates.

No Recent species truly referable to *Dimorphocella* has been reported before (see above), and the genus does not now seem to be represented in Australian seas. Fossil Australian colonies were erect and branched, but *D. moderna* resembles the fenestrate colonies of *Adeona*, which are found from the Australian Tertiary-to-Recent. These colonies reach a height and diameter of 25 cm, and are attached and supported by flexible rooting structures formed by alternating cuticular and calcified kenozooidal elements. Large colonies of *Adeona* also develop strengthening ribs by extrazooidal frontal calcification. At present, the attachment of both *D. moderna* and the fenestrate *Aspidostoma livida*, which were abundant at station SM 239, is unknown.

D. moderna closely resembles *D. triton*, differing in its colony form and the presence of fenestral avicularia.

Measurements (means of 20 values) in mm

Lz	lz	Lbr.z	lbr.z
0,61	0,35	0,69	0,53
Lor	lor	Lbr.or	l.br.or
0,15	0,13	0,06	0,21
Lad.av.	Lint.av		
0,24	0,45		
Lm	lm		
0,14	0,25		

Family **Exechonellidae** Harmer, 1957

Exechonellidae Harmer, 1957: 651.

Exechonella Duvergier, 1924

Exechonella Duvergier, 1924: 18, see Cheetham, 1966: 62. Canu & Bassler, 1927: 4. Cook, 1967: 337.

Exechonella sp.

Fig. 5G

Material

Stations SM 164, SM 185, SM 250.

Remarks

Only small and badly damaged colonies of this species were found. The zooids were up to 1,3 mm long by 0,9 mm broad, pyriform in shape with the distal end formed into a tubular peristome, broken short in all cases. The frontal wall consists of an umbonuloid shield perforated by large round pores, rimmed by concentric calcification, indicating that they are progressively infilled. Avicularia, spines and ovicells were not evident. Sufficient detail of the zooid morphology was preserved to suggest that this is a species of *Exechonella* (Cook 1967), but the material was too damaged to permit identification to species.

Family **Watersiporidae** Vigneaux, 1949

Watersiporidae Vigneaux, 1949: 15, 20.

The family includes genera with finely pseudoporous frontal shields and opercula with well-developed sclerites. Avicularia are usually absent, but polymorphic zooids may occur (Cook 1979). Ovicells are present in some species of *Pachycleithonia* but absent in other genera.

Pachycleithonia Canu & Bassler, 1930

Pachycleithonia Canu & Bassler, 1930: 25. Cook, 1983*b*.

Colonies encrusting. Zooids large; orifice with almost rectangular sinus and often massive condyles. Frontal cuticle and opercula dark brown or purple.

The affinities and general characters of the genus, which has a worldwide tropical and subtropical distribution, have been discussed by Cook (1983*b*). Ovicellate brooding zooids have not been described in the type species, *P. nigra* Canu & Bassler, from the Galapagos Islands, but distinctive, reticulate, hyperstomial ovicells are known in *P. mutabilis* and *P. africana*.

Pachycleithonia mutabilis (Canu & Bassler, 1929)

Fig. 14B

Galeopsis mutabilis (?partim) Canu & Bassler, 1929: 273, pl. 28 (figs 4–5), ?fig. 111A–B, *?non* pl. 28 (fig. 6).
Gigantopora mutabilis: Harmer, 1957: 883, pl. 40 (fig. 8).
Pachycleithonia mutabilis: Cook, 1983*b*.

Material

Stations SM 129, SM 131.

Description

Pachycleithonia with elongated tubular peristome and large peristomial spiramen. Zooids communicating by distal and lateral septula situated at the base of the vertical walls, surrounded by calcified buttresses. Frontal septula large: one pair on each side of the orifice, another pair at each lateral corner of the zooid. Ovicell hyperstomial not closed by the zooidal operculum; formed by a very thinly calcified, or wholly cuticular inner capsule derived from the maternal zooid, surrounded by a reticulate ooecial cover derived from the frontal shield of the distal zooid.

Remarks

The *Meiring Naude* material consists only of three small fragments, one of which has a single ovicell. Like many of the species described here, *P. mutabilis* is a relatively shallow-water form and these specimens represent transported debris. The elongated peristome, with its prominent spiramen, is easily damaged and is not present in all zooids.

Both Harmer (1957) and Cook (1983*b*) have noted that the material originally described by Canu & Bassler (1929) from the Philippine Islands appears to have comprised two species. One of these (Canu & Bassler 1929, pl. 28, figs 4–5) resembles the material described by Harmer (1957) from Indonesia, and also the *Meiring Naude* fragments; the other (pl. 28, fig. 6) has larger zooids and was described as having minute lateral oral avicularia. However, this latter photograph had been retouched, and it appears that the 'avicularia' are, in fact, the elongated cavities (areolae) above a distal pair of frontal septula. A. H. Cheetham (1979 *in litt.*) examined the original specimen and commented, 'They do appear to be aerolae, and . . . can be seen to lie above large septular openings'. The opercula figured by Canu & Bassler (1929, fig. 111A–B) might have originated from either or both of their specimens. The

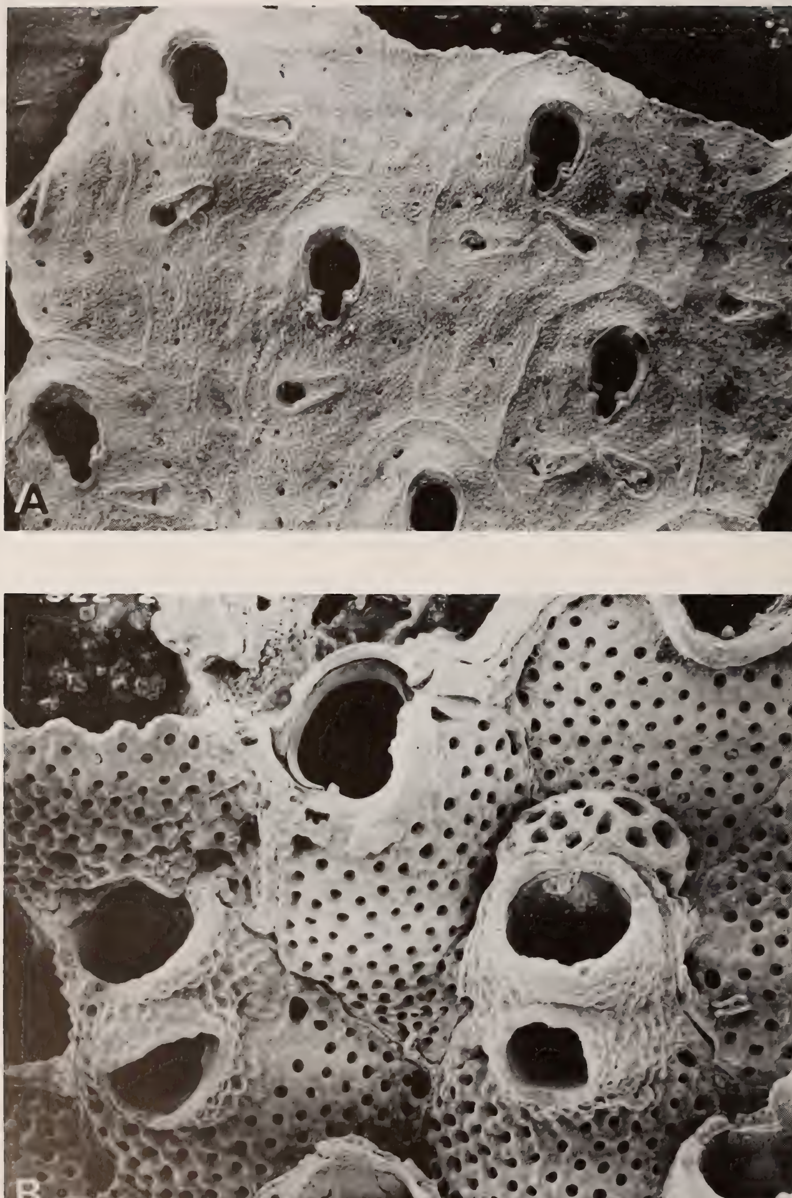

Fig. 14. A. *Dimorphocella submersa* (Waters). × 63. B. *Pachycleithonia mutabilis* (Canu & Bassler), BMNH 1882.10.18.46. × 64.

opercula of the *Siboga* specimens, and of a specimen from the Mascarene Islands (BMNH 1882.10.18.46), closely resemble those of *Watersipora arcuata* Banta (see Ryland 1974, fig. 3B), and those of the west African species *P. africana* Cook (1983*b*). *P. africana* is very similar to *P. mutabilis* in several other characters, and also has reticulate ovicells. Unlike *P. mutabilis*, however, the ovicell is closed by the operculum, and although the peristome is elongated it is not tubular and a spiramen rarely develops.

Distribution

P. mutabilis is known from the Philippines and Indonesia, Mauritius and south-east Africa.

Family **Euthyrisellidae** Bassler, 1953

Euthyrisellidae Bassler, 1953: G226.

Tropidozoum Harmer, 1957

Tropidozoum Harmer, 1957: 1106. Cook, 1975: 161. Cook & Chimonides, 1981*b*: 64.

Colonies rooted, cellariiform, internodes connected by cuticular keno-zooidal joints. Zooid frontal surfaces occupying only part of the curved face of the internode; the other side consisting of a column of extrazooidal coelom, limited by a cuticular wall. Frontal shields depressed, with foramina; hypostegal coelom on both sides of the calcification. Brooding zooids large, with inflated basal walls and dimorphic orifices. Avicularia absent.

The characters and relationships of this interesting genus are discussed by Cook & Chimonides (1981*b*).

Tropidozoum burrowsi Cook & Chimonides, 1981

Tropidozoum sp. Cook, 1975: 165, pl. 1 (*NB* explanation of pls. 1 and 3 transposed), fig. 2B.
Tropidozoum burrowsi Cook & Chimonides, 1981*b*: 65, figs 5–6, 10.

Material

Stations SM 131, SM 151.

Description

Tropidozoum with narrow basal coelom. Zooids with small frontal foramina; orifice with a deep triangular sinus. Orifice of brooding zooid wide, without a sinus.

Remarks

T. burrowsi is known to live in relatively shallow water (15 m), as does the closely related Indonesian species, *T. cellariiforme* Harmer. The worn internodes from stations SM 131 and SM 151 (780 m and 900 m respectively) have obviously been transported. Previous records from South Africa (BMNH

1949.11.10.184, off Durban, 90 m) were also of transported internodes, and it would appear that living colonies will eventually be found only in shallow or coastal waters.

Distribution

Madagascar and South Africa.

Family **Smittinidae** Levinsen, 1909

Smittinidae Levinsen, 1909: 335. Hayward & Ryland, 1979: 98.

Smittina Norman, 1903

Smittina Norman, 1903: 120. Hayward & Ryland, 1979: 98.

Smittina sitella sp. nov.

Fig. 15D–E

Material

Holotype: SAM–A26425, station SM 163, 33°04,6′S 28°06,6′E, 90 m.
Other material: stations SM 163, SM 163/164, SM 185, SM 239.

Description

Colony encrusting. Zooids oval, convex, separated by distinct grooves. Primary orifice slightly wider than long, proximal border largely occupied by a very broad lyrula, condyles small and generally inconspicuous. Peristome well developed, deep, distal border encroaching on to frontal surface of succeeding zooid, typically bearing one or two lateral lobes and incorporating medioproximally a conical avicularian cystid. Rostrum situated on distal face of cystid, elongate, triangular, acute to frontal plane. Adventitious avicularia also present adjacent to orifice, typically paired, occasionally single; cystid short, conical, rostrum directed laterally, or proximally, or oblique to either direction. Frontal wall finely granular with a few widely spaced pores, each becoming deeply immersed and conspicuous in later ontogeny. With the development of the suboral avicularium the pores proximal to the orifice become occluded and in highly calcified zooids frontal perforation appears to be limited to marginal areas. Ovicell hyperstomial, prominent, spherical, with regularly spaced pores. Ectooecium produced as a conspicuous frontal lip.

Etymology

Sitella (L.)—a little bucket, referring to the shape of the ovicell.

Measurements (means of 20 values) in mm

Lz	lz
0,67	0,44

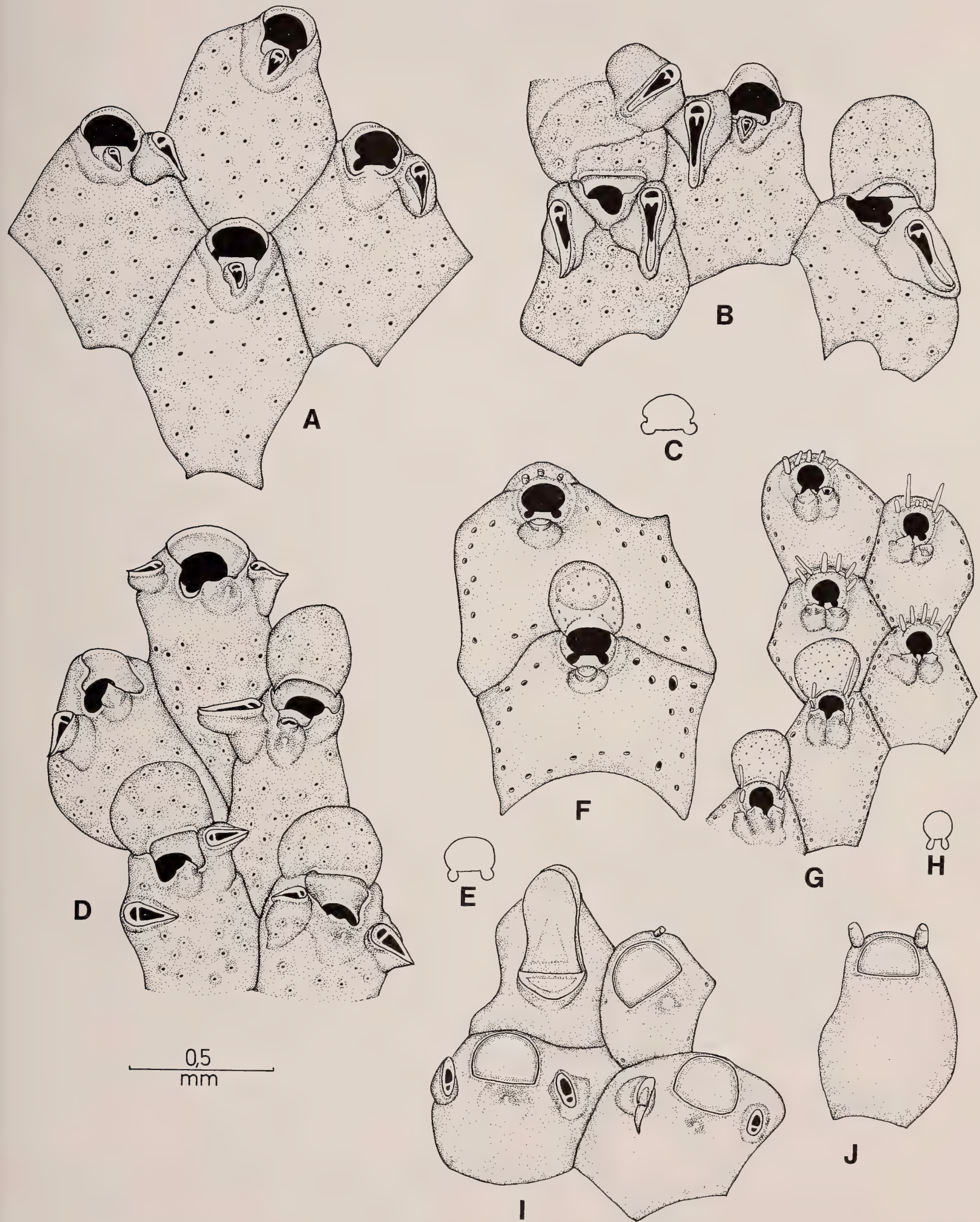

Fig. 15. A–C. *Smittina ferruginea* sp. nov. A. Zooids from the growing edge. B. Ovicelled zooids, with additional avicularia. C. Outline diagram of primary orifice. D–E. *Smittina sitella* sp. nov. D. A group of zooids, with ovicells and lateral avicularia. E. Outline diagram of primary orifice. F. *Smittoidea errata* sp. nov. G–H. *Smittoidea circumspecta* sp. nov. G. A group of zooids, with varying development of the suboral avicularia. H. Outline diagram of primary orifice. I–J. *Celleporaria capensis* (O'Donoghue & de Watteville). I. Three autozooids and a vicarious avicularium. J. A young zooid with oral spines intact.

Smittina ferruginea sp. nov.

Fig. 15A–C

Material

Holotype: SAM–A26426, station SM 239, 32°14,8′S 29°00,8′E, 90 m.

Description

Colony encrusting, multilaminar, forming broad irregular sheets. Zooids large, hexagonal, rather flat, separated by shallow grooves. Primary orifice subterminal, wider than long; lyrula broad and low, occupying greater part of proximal border, condyles short, quadrate, conspicuous. No oral spines. Peristome low, scarcely projecting above frontal surface of zooid; distal border formed from frontal calcification of succeeding zooid, incorporating proximally the cystid of a small, median suboral avicularium. Rostrum of avicularium triangular or semi-elliptical, partly enclosed within peristome, acute to frontal plane and directed proximally. Additional avicularia may be developed lateral to the peristome, single or paired; rostrum slender, elongate, straight or gently curved, typically directed proximally or obliquely proximally, rarely obliquely distal. Frontal wall finely granular, closely perforated by numerous round pores, each becoming immersed in a distinct pit as calcification continues. Ovicell hyperstomial, prominent, spherical, finely granular and regularly perforated by numerous small round pores; ectooecium forming a frontal lip continuous with the rim of the peristome.

Etymology

Ferruginus (L.)—rust-coloured.

Remarks

Several large well-grown colonies were collected from station SM 239, encrusting the living colony of *Aspidostoma livida*. The preserved material retained a dull purplish brown colour with scattered patches of deeper reddish brown. These patches corresponded to sites of active frontal budding, marking the development of new laminae, and the pigment was seen to be concentrated in the polypides of the young zooids, and in a narrow fringe around the undifferentiated growing edge of each lamina.

Measurements (means of 25 values) in mm

Lz	lz
0,87	0,58

Smittoidea Osburn, 1952

Smittoidea Osburn, 1952: 408. Hayward & Ryland, 1979: 108.

Smittoidea circumspecta sp. nov.

Fig. 15G–H

Material

Holotype: SAM–A26427, station SM 163, 33°04,6′S 28°06,6′E, 90 m.
Other material: stations SM 184, SM 185, SM 239.

Description

Colony encrusting, forming small round white patches. Zooids small, hexagonal, broad and convex, separated by deep grooves. Primary orifice longer than wide, distinctly narrowed proximally, with broad, basally deflected condyles; proximal border with a slender lyrula, fragile and frequently missing. Five or six slender closely spaced oral spines on the distal and lateral borders of the orifice; peristome scarcely developed, forming at the most a low lateral wall on each side. Suboral avicularium rarely single, typically twinned, frequently tripled or quadrupled; cystid short, cylindrical and erect, rostrum facing distally, perpendicular to frontal plane, mandible semicircular. The avicularian complex forms a two-, three-, or four-lobed digitate process immediately proximal to, and largely obscuring, the orifice. Frontal wall finely granular, with a single series of conspicuous marginal pores. Ovicell spherical, recumbent on succeeding zooid, with numerous small round pores.

Etymology

Circumspectus (L.)—guarded, an allusion to the oral avicularia.

Remarks

The elongate orifice, the closely spaced oral spines and the cluster of suboral avicularia impart a highly characteristic appearance to this species, which allows it to be readily distinguished from all other species of *Smittoidea*.

Measurements (means of 20 values) in mm

Lz	lz
0,46	0,37

Smittoidea errata sp. nov.

Fig. 15F

Smittoidea ?hexagonalis: Hayward & Cook, 1979: 89, fig. 12A–B.

Material

Holotype: SAM–A26428, station SM 163/164, 33°04,6′S 28°06,6′E, 90 m.
Other material: station SM 239.

Description

Colony encrusting. Zooids quadrate, flat or slightly convex, separated by distinct grooves. Primary orifice broader than long, with a short square lyrula occupying about half of the proximal border; condyles distinct, triangular, basally deflected. Three short distal oral spines present in newly budded zooids; peristome a low thickened rim enclosing orifice distally and laterally, proximally incorporating a small suboral avicularium. Mandible semicircular, acute to frontal plane, directed proximally. Occasionally replaced by an enlarged spatulate avicularium, directed proximolaterally (Hayward & Cook 1979). Frontal wall fine grained, with a series of marginal pores. Ovicell hyperstomial, recumbent on succeeding zooid; oval, thinly calcified, with about twenty small irregularly shaped frontal pores.

Etymology

Erratum (L.)—a mistake, referring to the previous misidentification of this species.

Remarks

The single specimen of this species collected from station SM 86 during the first *Meiring Naude* cruise (Hayward & Cook 1979) was erroneously ascribed to '*Smittina*' *hexagonalis* O'Donoghue 1924, which, in fact, lacks a suboral avicularium. Three small living colonies were present in the second collection, two of which were incubating embryos.

Measurements (means of 15 values) in mm

Lz	lz
0,67	0,51

Smittoidea calcarata sp. nov.

Fig. 16A–B

Material

Holotype: SAM–A26429, station SM 233, 32°15,2′S 29°09,8′E, 540–580 m.

Description

Colony encrusting, unilaminar, delicate and hyaline. Zooids flat and broad, irregularly polygonal, separated by shallow grooves. Primary orifice wider than long, proximal border with a tapered peg-like lyrula, condyles sharp, slender and conspicuous; distal border almost straight, two short distal oral spines visible in peripheral zooids, occluded by the development of succeeding zooids. Peristome short, erect, distal portion formed from the frontal calcification of the succeeding zooid, with a narrow, parallel-sided median fissure proximally. Avicularium situated immediately proximal to

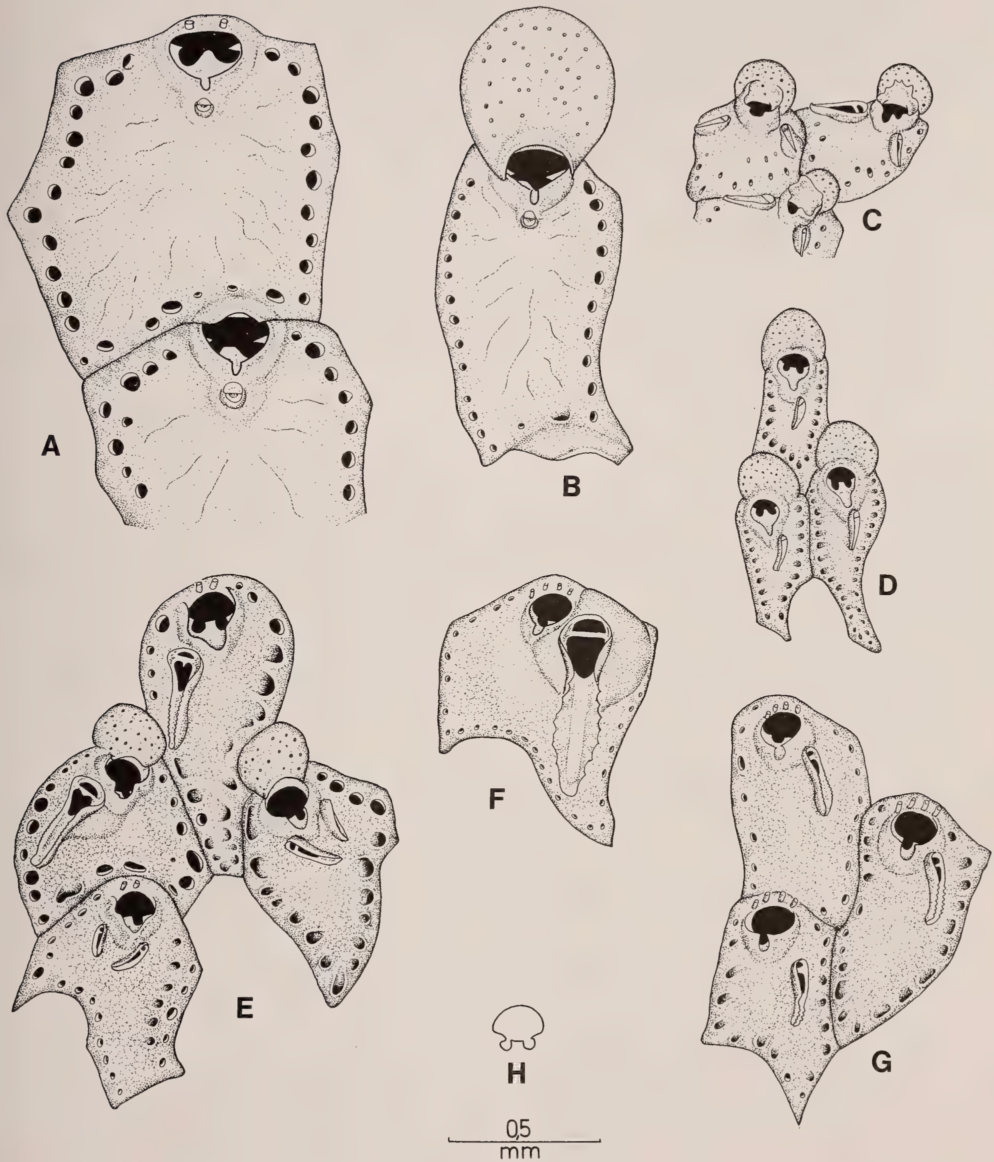

Fig. 16. A–B. *Smittoidea calcarata* sp. nov. A. Two zooids from close to the growing edge. B. An ovicelled zooid. C–D. *Parasmittina tropica* (Waters). C. Zooids with entire peristomes, showing different types of avicularia. D. Older zooids, with thickened peristomes. E–H. *Parasmittina novella* sp. nov. E. A group of zooids, with different types of avicularia. F. A zooid bearing an enlarged avicularium with flared serrate rostrum. G. Zooids with smaller avicularia, with serrate rostra. H. Outline diagram of primary orifice.

peristomial fissure, cystid low, rostrum elliptical, directed proximally, mandible semicircular. Frontal calcification thin, fine grained and sutured, with a single series of marginal pores. Ovicell oval, depressed frontally, developing a slight lip continuous with the zooid orifice; surface finely granular, with scattered, small, irregular pores.

Etymology

Calcar (L.)—a spur, referring to the sharp condyles within the primary orifice.

Remarks

A single large colony, measuring approximately 20 mm × 10 mm encrusting *Dimorphocella*, was collected from station SM 233.

Measurements (means of 15 values) in mm

Lz	lz
1,05	0,79

Parasmittina Osburn, 1952

Parasmittina Osburn, 1952: 411. Hayward & Ryland, 1979: 114.

Parasmittina tropica (Waters, 1909)

Fig. 16C–D

Smittia tropica Waters, 1909: 174, pl. 17 (figs 10–14).
Smittina tropica: Harmer, 1957: 934, pl. 64 (figs 23–28).
Parasmittina tropica: Cook, 1968: 215.

Material

Stations SM 163, SM 163/164, SM 164, SM 184, SM 185, SM 239.

Description

Colony encrusting. Zooids elongate, oval or irregular, rather flat. Primary orifice wider than long, a prominent quadrate lyrula occupying most of the proximal border, tapered distally to a greater or lesser extent; condyles large and conspicuous. Four short distal oral spines present in newly budded zooids. Peristome developing early in ontogeny, encircling primary orifice, and extending on to frontal surface of ovicell in fertile zooids; tubular, its edge variably lobed or produced. Proximomedially, the inner edge of the peristome develops a pair of longitudinal ridges delimiting a central channel, which in damaged specimens gives the illusion of a sinuate orifice. Frontal wall nodular, with a single series of large and distinct marginal pores. Adventitious avicularium arising laterally at base of peristome, directed proximally, laterally or medially, typically single, occasionally, paired; rostrum slender, elongate, up

to 0,15 mm long. Ovicell spherical, with numerous small pores; recumbent on succeeding zooid and eventually deriving an ooecial cover from it.

Remarks

Parasmittina tropica is readily distinguished from other species of this genus by the form of the peristome and by the characteristically slender avicularia. Some specimens included zooids bearing a second type of avicularium, broader proximally than the usual type (Fig. 16C), but as the latter frequently occurred on the same zooids also, this variation does not seem to be significant. The lyrula also varied greatly in width, but again such variation was observed within single colonies. In the structure of the peristome and the presence of slender parallel-sided avicularia all the numerous specimens here ascribed to *P. tropica* are closely similar.

Distribution

Described originally from the Red Sea coast of the Sudan (Waters 1909), this species has subsequently been reported from west Africa (Cook 1968) and the Mediterranean (Hayward 1974), and was accorded a wide distribution in the Indo-West-Pacific region by Harmer (1957). Soule & Soule (1973) have shown that some of Harmer's material comprises a distinct species, *P. serrula* Soule & Soule, and, consequently, the distribution of *P. tropica* may be more restricted than Harmer supposed.

Measurements (means of 20 values) in mm

Lz	lz
0,54	0,28

Parasmittina novella sp. nov.

Fig. 16E–H

Material

Holotype: SAM–A26430, station SM 239, 32°14,8′S 29°00,8′E, 90 m.

Description

Colony encrusting, multilaminar. Zooids oval, rectangûlar or irregular, convex, separated by shallow grooves. Primary orifice wider than long, lyrula short, anvil-shaped, occupying half width of proximal edge, condyles blunt, broad and conspicuous; two to four short, evanescent, distal oral spines, bases occluded by development of peristome. Distal portion of peristome developed from frontal calcification of succeeding zooid; prominent laterally and proximally, thin and erect, with a deep, parallel-sided medioproximal fissure; extending on to frontal surface of ovicell in fertile zooids, forming a complete ring. Free edge of peristome even or lobed. Frontal calcification at first smooth and hyaline, with a single series of small inconspicuous marginal pores; later

thicker and rather nodular. Avicularia lateral or proximolateral to peristome, single, paired or occasionally tripled, directed proximally; rostrum slender, parallel-sided and straight, or gently curved, up to 0,17 mm long, palate with a triangular foramen, pivotal bar thin, without a columella. In many, but not all, instances the distal edges of the rostrum are slightly flared and distinctly serrate (Fig. 16G). A larger avicularium may be developed on one side of the zooid, with an elongate, proximally directed rostrum up to 0,4 mm long; the rostrum is variably flared distally with fine or coarse serrations. Ovicell small, spherical, recumbent on distally succeeding zooid, surface finely granular, with numerous small pores.

Etymology

Novus (L.)—new.

Remarks

Parasmittina novella differs most markedly from *P. tropica* (Waters) and from the eastern Pacific *P. serrula* Soule & Soule in the size of its zooids; for the latter species Soule & Soule (1973) gave mean dimensions of Lz 0,368 mm, lz 0,284 mm, while the zooids of *P. novella* were 0,6–1,0 mm long and 0,38–0,6 mm wide. Although the two species are similar in possessing avicularia with flared serrate rostra, those of *P. serrula* seem to be less variable in all respects than those of *P. novella*. Both species resemble *P. tropica* in the form of the peristome, but in *P. novella* this is a far more delicate structure, lacking the proximal longitudinal thickening and sinuate appearance of Waters's species.

Measurements (means of 40 values) in mm

Lz	lz
0,74	0,44

Porella Gray, 1848

Porella Gray, 1848: 127, 148. Hayward & Ryland, 1979: 116.

Porella capensis O'Donoghue, 1924

Fig. 17A–B

Porella capensis O'Donoghue, 1924: 45, pl. 2 (fig. 14).

Material

Stations SM 163, SM 164, SM 239.

Remarks

Several small colonies of this species were found, occurring as irregular encrusting patches on organic calcareous substrata. The characteristic peristome clearly develops, as O'Donoghue (1924) described, as separate elements,

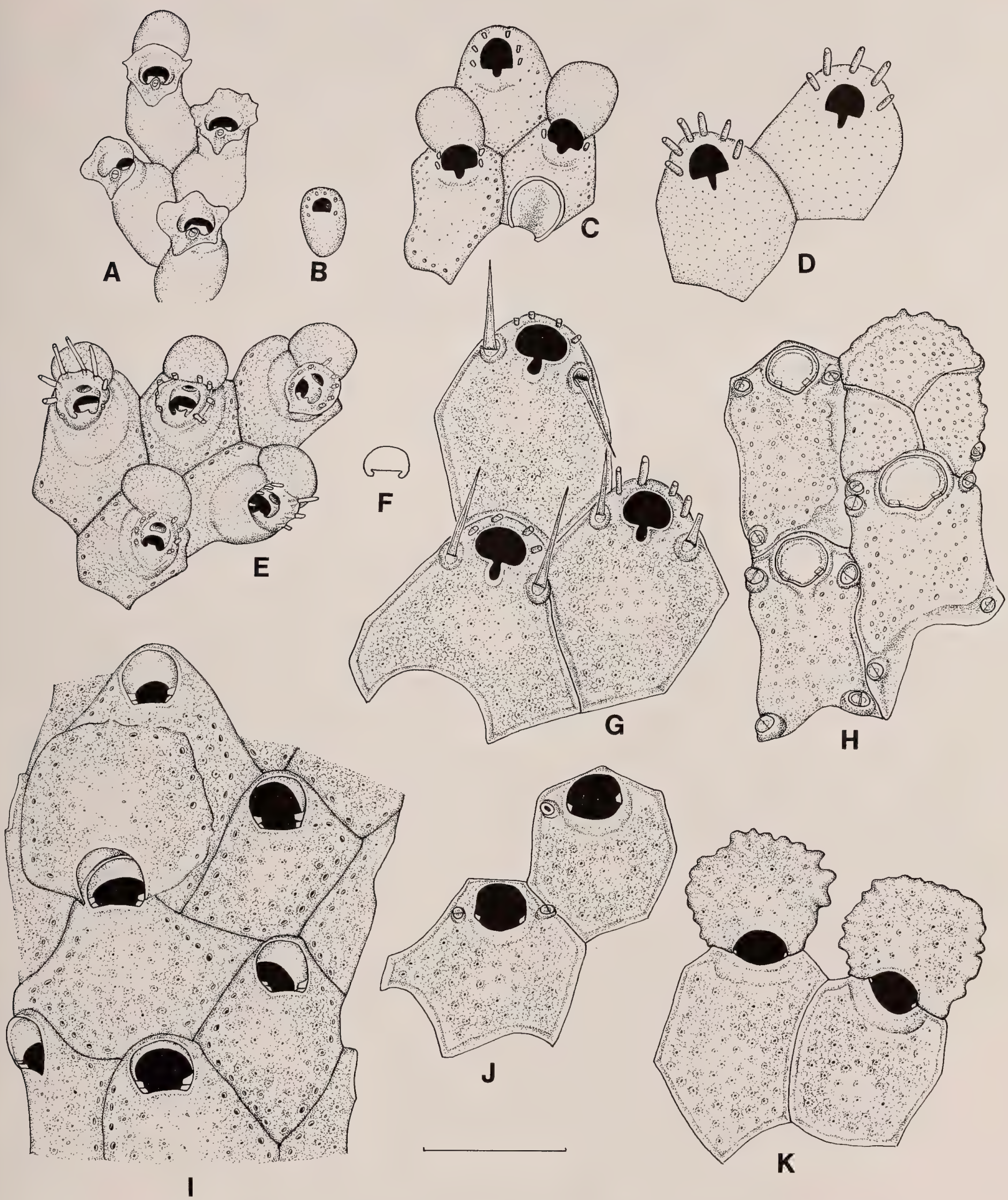

Fig. 17. A–B. *Porella capensis* O'Donoghue. A. Zooids with typical development of peristome; note the lyrula. B. The ancestrula. C. *Arthropoma circinatum* (MacGillivray). D. *Arthropoma* sp. E–F. *Escharella discors* sp. nov. E. Part of a colony, cleaned to show the lyrula below the peristomial denticle. F. Outline diagram of primary orifice. G. *Escharina waiparaensis* Brown. H. *Calyptotheca nivea* (Busk). I. *Emballotheca ambigua* sp. nov. J–K. *Calyptotheca porelliformis* (Waters). J. Two young zooids. K. Two ovicelled zooids. Scale = 0,5 mm for A–H, J–K; 1 mm for I.

a broad flared proximolateral portion and two distolateral portions. Small adventitious avicularia may occur on the distolateral parts of the peristome rim, but the specimens were too worn or damaged for further details to be observed. The lyrula, not described by O'Donoghue, is quadrate and quite distinct.

Family **Escharellidae** Levinsen, 1909

Escharellidae Levinsen, 1909: 314. Hayward & Ryland, 1979: 136.

Escharella Gray, 1848

Escharella Gray, 1848: 125, 148. Hayward & Ryland, 1979: 136.

Escharella discors sp. nov.

Fig. 17E–F

Material

Holotype: SAM–A26431, station SM 163/164, 33°04,6′S 28°06,6′E, 90 m.

Description

Colony encrusting, forming small irregular white patches. Zooids small, oval, convex, separated by deep grooves. Primary orifice wider than long, proximal border with a broad anvil-shaped lyrula occupying the whole of its width; encircled by a tall, thickened, cylindrical peristome, with eight slender spines disposed around its distal and lateral edges. Proximal edge of peristome peaked medially and bearing a bifurcate denticle on its inner face. Frontal wall thickly calcified, finely granular, marginal pores small and rather conspicuous. Ovicell spherical, tilted basally, the oval orifice opening into the top of the peristome.

Etymology

Discors (L.)—different.

Remarks

The morphology of the primary orifice and the number of oral spines are the most useful characters for distinguishing the different species of *Escharella*. *E. discors* has a further distinction in the large and conspicuous peristomial denticle, which in uncleaned specimens may be confused with the lyrula.

Measurements (means of 20 values) in mm

Lz	lz
0,51	0,31

Family **Petraliellidae** Harmer, 1957

Petraliellidae Harmer, 1957: 692.

The family includes a closely related group of genera, all of which are characterized by zooids with large orifices, and frontal shields with pseudopores

and marginal septula. Multiporous septula in the basal walls give rise to anchoring rhizoids; large distinctive, hyperstomial ovicells occur (see Cook & Chimonides 1981*a*).

Mucropetraliella Stach, 1936

Mucropetraliella Stach, 1936: 363, 372. Harmer, 1957: 709. Cook & Chimonides, 1981*a*: 118.

Characterized principally by the presence of a suboral complex consisting of a central lyrula and a mucro associated with an avicularium.

Mucropetraliella asymmetrica sp. nov.

Fig. 18

Material

Holotype: SAM–A26432, station SM 239, 32°14,8′S 29°00,8′E, 90 m.
Other material: stations SM 163, SM 164, SM 179, SM 180, SM 185.

Description

Colonies unilaminar, loosely encrusting, anchored by rhizoids originating from basal pore plates. Primary orifice wide, with two to three spines. Lyrula short and wide, sometimes extended laterally; lateral denticles pointing proximally. Lateral sinuses unequal and asymmetrical, the larger one occurring basally to the rostrum of the avicularium. Suboral mucro long and very stout; proximal part of the orifice and the frontal shield considerably raised. Suboral avicularium small, completely hidden at the base of the mucro, which is directed frontally and distally; rostrum curved, directed laterally, palate vertical to frontal plane, mandible rounded, hinged on a stout curved bar and directed medially. One or two pairs of small lateral oral avicularia present, also with rounded mandibles, directed laterally at an acute angle to frontal plane. In a few zooids other small rounded avicularia occur at the base of the mucro; one of the oral avicularia may be enlarged, with a conspicuous swollen cystid, the rostrum raised, with a serrated edge, elongate and slightly spatulate, often orientated proximally. Ovicells rather elongated, finely tuberculate, with one or two small frontal avicularia.

Etymology

Asymmetros (Gr.)—without symmetry, referring to the suboral sinuses.

Remarks

The lyrula and suboral avicularium are difficult to see as they are situated vertically below the mucro, which may reach a length of 1,2 mm and frequently obscures the orifice completely. *M. asymmetrica* closely resembles *M. watersi* Harmer (1957: 721, pl. 46 (fig. 9), fig. 67, from the East Indies), which was introduced for *Petralia vultur* var. *armata* Waters (1913: 518, pl. 70 (figs 15–20), from east Africa). Harmer noted that synonymy of the two species might be

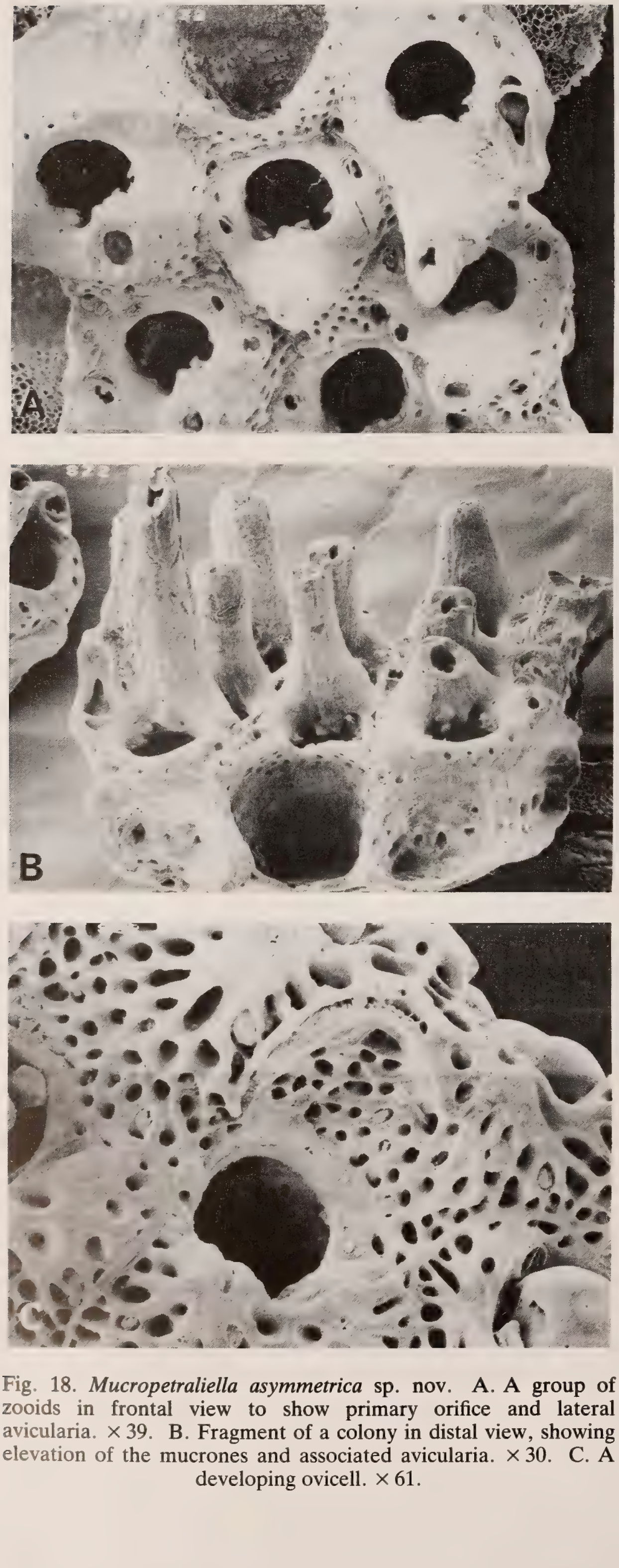

Fig. 18. *Mucropetraliella asymmetrica* sp. nov. A. A group of zooids in frontal view to show primary orifice and lateral avicularia. × 39. B. Fragment of a colony in distal view, showing elevation of the mucrones and associated avicularia. × 30. C. A developing ovicell. × 61.

doubted as Waters did not mention oral spines in his description. Comparison of the Siboga specimens described by Harmer (1957) with one from the coast of Kenya (BMNH 1975.4.16.5) shows them to be closely similar. The zooids of *M. watersi* are less robust than those of *M. asymmetrica* and somewhat smaller (Lz 0,85–1,0 mm, lz 0,55–0,65 mm, lor 0,24–0,31 mm); the primary orifice has four to six spines and symmetrical, equally developed lateral sinuses. The proximal part of the orifice is not greatly raised and the suboral complex is easily visible. Enlarged laterally or proximally directed avicularia are common and ovicells are generally as wide or wider than long (cf. Harmer 1957).

Although most of the specimens of *M. asymmetrica* are fragmentary and often worn, one colony from station SM 239, and another very young colony (with *Micropora similis*) on a lamellibranch shell from station SM 164 were alive when collected.

Measurements in mm

(range of 10 values)

Lz	lz	lor
0,85–1,30	0,60–0,90	0,30–0,42

(means of 3 values)

Lov	lov
0,55	0,52

Family **Schizoporellidae** Jullien, 1883

Schizoporellidae Jullien, 1883: 527. Hayward & Ryland, 1979: 166.

Arthropoma Levinsen, 1909

Arthropoma Levinsen, 1909: 332. Hayward & Ryland, 1979: 190.

Arthropoma cecilii (Audouin, 1826)

Flustra cecilii Audouin, 1826: 239, pl. 8 (fig. 3).
Schizoporella cecilii: O'Donoghue, 1924: 42.
Arthropoma cecilii: Hayward & Ryland, 1979: 190, fig. 79.

Material

Station SM 185.

Remarks

A single live colony of this species was found. *A cecilii* has a wide distribution in temperate, subtropical and tropical waters of the Atlantic, Indian and western Pacific oceans.

Arthropoma circinatum (MacGillivray, 1869)

Fig. 17C

Lepralia circinata MacGillivray, 1869: 134.
Arthropoma circinatum: Harmer, 1957: 1003, pl. 72 (figs 29–30). Powell, 1967: 256, text-figs 29–30.

Material

Station SM 163.

Description

Colony encrusting. Zooids hexagonal, convex, separated by deep grooves; 0,46–0,5 mm long by 0,34–0,4 mm broad. Primary orifice D-shaped, proximal border straight or slightly concave, with a short, quadrate median sinus. Six oral spines present. Frontal wall finely granular, with distinct marginal pores, extending towards the midline of the zooid proximolateral to orifice; elsewhere, minute scattered pores are occasionally visible in the frontal calcification. Peristome forming a slender crescentic lip proximal to the sinus, variably developed. Ovicell hyperstomial, prominent, spherical; surface finely granular, imperforate.

Remarks

A single dead colony was found, few of the zooids of which were completely undamaged. The morphological features of this specimen were very similar to those of specimens from New Zealand (BMNH 1899.5.1.1017) and Bass Strait (BMNH 1899.5.1.1018), although the New Zealand specimen has avicularia identical to those figured by Powell (1967, fig. 30) for '*A. circinatum* form B'. No complete avicularia were found in the *Meiring Naude* specimen, but a damaged zooid at the periphery of the colony bore a structure on the frontal wall which seemed to represent a developing 'form B' avicularium.

Distribution

Arthropoma circinatum seems to be widespread in the western Pacific, from New Zealand to Japan (Harmer 1957; Powell 1967), and has been reported from Tristan da Cunha (Busk 1884) and southern California (Osburn 1952). The record from Ceylon listed by Harmer (1957: 1004) is based on a specimen from the collection of L. R. Thornely that, on examination, proved to be a species of *Schizomavella*.

Arthropoma sp.

Fig. 17D

Material

Stations SM 163, SM 185.

Remarks

Very small colonies of this species were recovered from two stations. Although superficially similar to *A. cecilii*, the zooids differed in possessing five or six distal oral spines, and a smaller orifice with a more slender sinus. However, the material was fragmentary and none of the colonies represented a complete astogenetic series. Consequently, although its affinities with *Arthropoma* seem clear, this species must remain unnamed until further material is collected.

Escharina Milne Edwards, 1836

Escharina Milne Edwards, 1836: 230. Hayward & Ryland, 1979: 192.

Escharina pesanseris (Smitt, 1873)

Hippothoa pesanseris Smitt, 1873: 43, 76, pl. 7 (figs 159–160).
Escharina pesanseris: Harmer, 1957: 998, pl. 67 (figs 12–14, 18–19).

Material

Station SM 250.

Remarks

A single live colony of this distinctive species was collected; it is recognized by the characteristic duck-foot shape of the avicularian mandible (Harmer, 1957: pl. 67 (fig. 12)). *Escharina pesanseris* has been reported from numerous localities in the Caribbean, the subtropical-tropical Atlantic, and the Indo-West-Pacific region. It is known from Ceylon and Madagascar but does not seem to have been recorded before from South Africa.

Escharina waiparaensis Brown, 1952

Fig. 17G

Escharina waiparaensis Brown, 1952: 229, figs 163–165. Powell, 1967: 275, pl. 6 (fig. a), text-fig. 45.

Material

Stations SM 164, SM 239.

Description

Colony encrusting. Zooids broad and flat, rounded distally, separated by raised, compressed sutures. Primary orifice wider than long; anter semiorbicular, with a slightly convex proximal border, poster slender, slit-like, broadening proximally. Four short distal oral spines present. Frontal wall coarsely granular, perforated by numerous closely spaced, minute pores. Avicularia paired, lateral to orifice, level with the sinus; cystid small and rounded, supporting an elongate, distally directed, setiform mandible. Ovicells were not found. Numerous small basal pore chambers present.

Remarks

E. waiparaensis was described by Brown (1952) from the Miocene and Pliocene of New Zealand; recent specimens were reported by Powell (1967) from Three Kings Islands, northern New Zealand. Brown's material lacked spines, but Powell described two distal oral spines and two lateral 'eminences', possibly representing thickened spine bases. The *Meiring Naude* material, which included several living colonies, had four lightly calcified oral spines in the youngest zooids, but the ontogenetically earliest zooids lacked spines

altogether. In all respects the present material was identical with Powell's specimens from Three Kings Islands (BMNH 1964.8.12.59C, 59D).

Measurements (means of 20 values) in mm

Lz	lz
0,72	0,63

Calyptotheca Harmer, 1957

Calyptotheca Harmer, 1957: 1008.

Calyptotheca nivea (Busk, 1884)

Fig. 17H

Schizoporella nivea Busk, 1884: 163, pl. 17 (fig. 1). Marcus, 1922: 25, fig. 15.
Schizoporella tenuis: O'Donoghue & De Watteville, 1935: 214.
Emballotheca nivea: O'Donoghue & De Watteville, 1944: 424. O' Donoghue, 1957: 87.

Material

Stations SM 163, SM 163/164, SM 164, SM 179, SM 185, SM 232.

Description

Colony encrusting, multilaminar. Zooids quadrate, broad, flat or slightly convex, separated by distinct raised sutures; 0,5–0,8 mm long by 0,38–0,52 mm broad. Primary orifice subterminal, orbicular, as wide as long, or slightly wider than long; poster forming a shallow U-shaped sinus below conspicuous quadrate lateral condyles. Frontal wall regularly and closely perforated by numerous round pores, each in a shallow pit, giving a rugose appearance. Avicularia adventitious, small, typically paired, situated lateral to orifice, close to suture of zooid; mandible semi-elliptical, short, variably orientated. Ovicell hyperstomial, closed by zooidal operculum; oval, flattened frontally, regularly perforated and typically crossed by sutures. Orifice of ovicelled zooid broader than that of non-fertile zooid, with a wider and more shallow sinus.

The shape of the primary orifice showed some variation between the different specimens, and earlier astogenetic stages tended to have a more narrow sinus. In the colony from station SM 185 the zooids had developed short cylindrical umbones proximal to the orifice, like those of the specimen figured by Marcus (1922). The small avicularia are often very numerous, but tend to be distributed along the interzooidal sutures.

Distribution

Calyptotheca nivea seems to be known only from the southern and eastern coasts of South Africa. Reports of its occurrence elsewhere in the Indo-West-Pacific region have been shown by Harmer (1957) to be attributable to other species of *Calyptotheca*.

Calyptotheca porelliformis (Waters, 1918)

Fig. 17J–K

Schizoporella porelliformis Waters, 1918: 15 (footnote), pl. 2 (figs 19–21).
Calyptotheca porelliformis: Harmer, 1957: 1008, 1020.

Material

Stations SM 163, SM 185.

Description

Colony encrusting, multilaminar. Zooids broad, quadrate, flat or slightly convex, separated by distinct raised sutures; 0,56–0,76 mm long by 0,4–0,6 mm broad. Primary orifice as broad as long, anter and poster of equivalent length; anter D-shaped, poster shallowly concave, condyles prominent, blunt and downcurved. Frontal wall rugose, regularly and closely punctured by numerous round pores, each in a pit; a low, nodular ridge develops around proximal half of orifice. Avicularia adventitious, minute, oval, with semi-elliptical mandible; infrequent, situated lateral to orifice, close to sutures, single or paired, but often absent altogether. Ovicell recumbent on succeeding zooid, hyperstomial, closed by zooidal operculum; oval, flat frontally, closely punctured and very rugose. Anter of ovicelled zooids much shorter than that of non-ovicelled zooids.

Distribution

This species does not seem to have been reported since its original description by Waters (1918) from Port Elizabeth.

Emballotheca Levinsen, 1909

Emballotheca Levinsen, 1909: 89, 333. Harmer, 1957: 1086.

Emballotheca ambigua sp. nov.

Fig. 17I

Material

Holotype: SAM–A26433, station SM 250, 31°59,3′S 29°22,5′E, 150–200 m.

Description

Colony erect, dichotomously branching; branches cylindrical, somewhat uneven or curved, about 2,5 mm thick, composed of whorls of four zooids. Zooids large and broad, convex, separated by faint sutures. Frontal calcification thick, finely granular, with numerous small closely spaced pores and a single series of more distinct marginal pores. A conspicuous thick light brown epitheca present. Primary orifice broader than long; anter approximately semicircular, poster forming a shallow semi-elliptical trough between short

blunt lateral condyles. In fully developed, undamaged zooids the condyles appear twinned (Fig. 17I). Ovicell very large, immersed and scarcely protruding from branch surface, obscuring most of the distally succeeding zooid, but not disturbing the four-whorled arrangement; orifice of ovicelled zooid enlarged, more nearly quadrate, with the poster considerably broadened.

Etymology

Ambiguus (L.)—uncertain, referring to the systematic placing of the species.

Remarks

The material comprised two fragments, each 15 mm long; both were living when collected and perhaps represent parts of a single colony. The very large ovicells, dimorphic orifices and prominent condyles of this species suggest it is allied to the species of *Emballotheca* described by Harmer (1957). However, it should be noted that the distinction between this genus and *Calyptotheca* Harmer is unclear (see Dumont 1981), and the systematic placing of *E. ambigua* must, therefore, be regarded as tentative.

Measurements (means of 20 values) in mm

Lz	Lor	lor
1,42	0,35	0,36

Family **Stomachetosellidae** Canu & Bassler, 1917

Stomachetosellidae Canu & Bassler, 1917: 44. Hayward & Ryland, 1979: 208.

Stomachetosella Canu & Bassler, 1917

Stomachetosella Canu & Bassler, 1917: 45. Hayward & Ryland, 1979: 208.

Stomachetosella balani (O'Donoghue & De Watteville, 1944)

Schizoporella balani O'Donoghue & De Watteville, 1944: 426, pl. 16 (figs 15–16).
Stomachetosella balani: O'Donoghue, 1957: 87.
Schizoporella balani: Hayward, 1980: 705, fig. 3G.

Material

Station SM 185.

Remarks

This characteristic South African species was recently redescribed and figured by Hayward (1980). Its affinities with the boreal Atlantic species currently assigned to *Stomachetosella* seem doubtful, and the relationship of all Recent species to the type species, *S. crassicollis* Canu & Bassler, requires re-examination. *S. balani* appears more similar to the Philippine species, *Schizoporella perforata* Canu & Bassler (1929: 318), than to other species of *Stomachetosella*.

Family **Cleidochasmatidae** Cheetham & Sandberg, 1964

Cleidochasmatidae Cheetham & Sandberg, 1964: 1032.

Systematic problems involving species within this family are reviewed on p. 104.

Cleidochasma Harmer, 1957

Cleidochasma Harmer, 1957: 1032. Cook, 1964*b*: 11.

Cleidochasma porcellanum (Busk, 1860)

Lepralia porcellana Busk, 1860: 283, pl. 31 (fig. 3).
Cleidochasma porcellanum: Cook, 1964*b*: 11, pl. 1 (fig. 4), pl. 2 (figs 1–2), fig. 4A–E.

Material

Station SM 163.

Description

Colony encrusting, zooids with imperforate, semi-transparent porcellanous frontal shields and four small marginal septula. Orifice rounded distally, with a small rounded sinus delineated by large proximally directed condyles. Avicularia small, often paired, lateral and suboral, mandible rounded or subtriangular, directed laterally; if not present, avicularium replaced by one of the marginal septula. Ovicells hyaline and prominent at first, hyperstomial, not closed by the operculum, becoming partially immersed. Proximal edge of ovicell with paired lateral indentations and an area of thin calcification.

Remarks

A single, fairly large colony, comprising approximately 1 250 zooids, was found. It was alive when collected, and includes a well-preserved growing edge. The earlier stages of colony growth are obscured by small groups of frontally budded zooids. The orifice is more elongated than those of east African specimens (BMNH 1976.7.20.7, Wasin, Zanzibar) and of the west African specimens illustrated by Cook (1964*b*).

C. porcellanum is a widely distributed and very variable species-complex which includes *C. bassleri* (Calvet), as described by Harmer (1957). Records are circumtropical and subtropical, with a depth range of 1–220 m.

Cleidochasma protrusum (Thornely, 1905)

Gemellipora protrusa Thornely, 1905: 119, pl. 7.
Cleidochasma protrusum: Harmer, 1957: 1040, pl. 71 (figs 1–4), fig. 112. Hayward & Cook, 1979: 89.

Material

Station SM 131.

Remarks

A single, small dead colony was found. The characteristic morphotype of the South African populations of *C. protrusum* was noted by Hayward & Cook (1979).

Cleidochasma cribritheca (Busk, 1884)

Fig. 19A

Gemellipora cribritheca Busk, 1884: 176, pl. 33 (fig. 5).

Material

Stations SM 163, SM 163/164, SM 164.

Description

Colony encrusting, unilaminar, appearing white and porcellanous. Zooids oval to hexagonal, convex, separated by shallow grooves; 0,4–0,6 mm long by 0,2–0,3 mm broad. Primary orifice longer than wide, anter suborbicular, poster elongate, V-shaped; condyles prominent, proximally directed. Orifice becoming immersed as calcification thickens, but without a defined peristome; no oral spines. Frontal wall at first smooth, with numerous small frontal pores; becoming more rugose in later ontogenetic stages, with pores sunk in small pits. Avicularium single, proximal to sinus, on a small tumid cystid; mandible semi-elliptical or semicircular, directed proximally. Ovicell recumbent on succeeding zooid, oval, flattened frontally and perforated by numerous small pores; later enveloped distally and laterally by a thickened ooecial cover.

A colony from SM 163 (Fig. 19A) included early astogenetic stages. These were partly obscured by later zooids but showed clearly two small zooids, each with numerous small oral spines. These may represent a twinned ancestrula; alternatively, the ancestrula may be obscured by the two largest zooids and the small zooids may be simply the first to be budded from the ancestrula.

Distribution

This species is known only from South African waters.

Cleidochasma perspicua sp. nov.

Fig. 19B

Material

Holotype: SAM–A26434, station SM 163, 33°04,6′S 28°06,6′E, 90 m.

Description

Colony encrusting. Zooids hexagonal, convex, separated by shallow grooves. Primary orifice cleithridiate: anter orbicular, poster wider than long, V-shaped, condyles large and distinct, blunt, basally deflected. Peristome

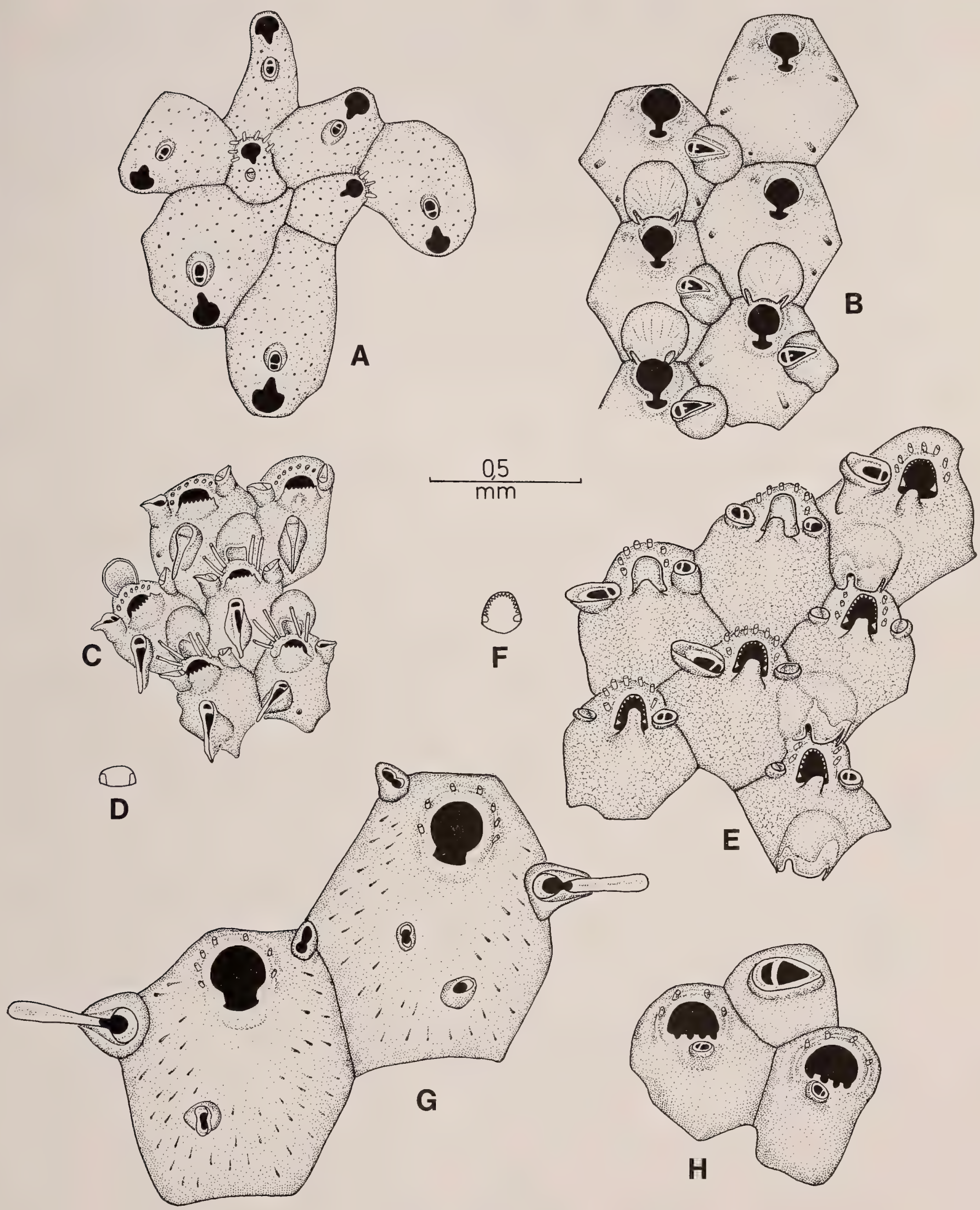

Fig. 19. A. *Cleidochasma cribritheca* (Busk). B. *Cleidochasma perspicua* sp. nov. C–D. *Hippoporella spinigera* (Philipps). C. Portion of a young colony. D. Outline diagram of primary orifice. E–F. *Hippoporella labiata* sp. nov. E. Portion of a young colony. F. Outline diagram of primary orifice. G. *Hippomenella avicularis* (Livingstone). H. *Celleporaria tridenticulata* (Busk).

developed as a low rim distally and laterally, frequently with two or more short umbones laterally; a third small umbo may be developed proximal to the orifice. Frontal wall thick, vitreous, smooth, with very few sparsely distributed and indistinct marginal pores; thick, translucent secondary calcification infills the grooves between zooids in later ontogenetic stages, pore openings migrate medially as this encroaches and the passage of the pore appears tubular (Fig. 19B). Avicularium adventitious, single, proximolateral to orifice; cystid tumid, rostrum slender, acute triangular, directed obliquely laterally, palate with a triangular foramen, cross-bar stout with a thickened, quadrate columella. The avicularia are sporadically developed, frequently missing from many zooids. Ovicell recumbent on succeeding zooid, as wide as long, flattened frontally and with a distinct labellum; calcification smooth and imperforate, developing a small median umbo. Large basal pore chambers present.

Etymology

Perspicuus (L.)—transparent, an allusion to the frontal calcification.

Remarks

The holotype comprises a single unilaminar colony, 5 mm^2 in area. It was alive when collected and many of the ovicells contained embryos. *C. perspicua* is most similar to *C. porcellanum* (Busk), which appears to have a circumtropical distribution. In particular, the primary orifice of this species is very similar to that of a variant of *C. porcellanum* from Ceylon, illustrated by Cook (1964*b*, text-fig. 4). However, the large tumid avicularian cystids and the conspicuous frontal labellum of the ovicell are sufficient to distinguish *C. perspicua* from other species of *Cleidochasma*. For further discussion of this species see p. 104.

Measurements (means of 20 values) in mm

Lz	lz
0,45	0,4

Hippoporidra Canu & Bassler, 1927

Hippoporidra Canu & Bassler 1927: 21, 31. Cook, 1964*b*: 22. Taylor & Cook, 1981: 244.

Hippoporidra senegambiensis (Carter, 1882)

Cellepora senegambiensis Carter, 1882: 416, pl. 16 (fig. 1A–V).
Hippoporidra senegambiensis: Cook, 1964*b*: 29, pl. 3 (figs 3–4), figs 7B–C, 8A–D; 1968: 196, 4pl. 8 (fig. C).

Material

Station SM 185, one young colony on *Turritigera* shell.

Description

Colonies encrusting gastropod shells, usually those inhabited by pagurid crabs. Zooids multilamellar, produced by frontal budding, with two to four

series of frontal marginal septula and orifices with rounded sinus and distinct condyles. Colony becoming mamillate by budding of groups of prominent, large (?male) zooids with small orifices and tuberculate peristomes. Interzooidal and adventitious avicularia triangular or rounded. Ovicelled zooids occurring in hollows among the mamillae, ovicells with a small frontal area.

Remarks

H. senegambiensis is common in west African waters, to a depth of 100 m. The single specimen found, which encrusts a small *Turritigera* shell 10 mm in length, is a young colony without ovicells that was alive when collected. Another species of *Hippoporidra*, *H. picardi*, has been reported from South Africa from depths of 45 to 200 m. *H. picardi* has larger, more recumbent zooids, with orifices having a small rounded sinus.

Hippoporella Canu, 1917

Hippoporella Canu, 1917: 36. Harmer, 1957: 1096. Hayward & Ryland, 1979: 218.

Hippoporella spinigera (Philipps, 1899)

Fig. 19C–D

Escharoides spinigera Philipps, 1899: 440, 448, pl. 43 (fig. 12).
Hippoporella spinigera: Harmer, 1957: 1100, pl. 73 (fig. 13).
Mucronella serratilabris O'Donoghue, 1924: 48, pl. 3 (fig. 18).

Material

Stations SM 131, SM 151, SM 163, SM 164, SM 250.

Description

Colony encrusting, forming small circular, silvery patches. Zooids oval to hexagonal, small and rather broad; separated by shallow grooves, later obscured by calcification. Primary orifice broader than long, appearing rather quadrate; distal edge arched, proximal edge almost straight, blunt lateral condyles present. Seven long, slender, closely grouped distal oral spines. Peristome developed proximally as a blunt, prominent mucro, with a broad, quadrate, finely serrated lip on its distal edge. Adventitious avicularia paired, lateral to orifice; mandible acute triangular, directed laterally or distolaterally. Additional avicularia present on frontal wall: most frequently elongate, situated on midline of zooid, with slender triangular mandible directed proximally; more rarely, one or two avicularia, similar to oral type but slightly larger, situated elsewhere on frontal wall, with variable orientation. Frontal wall smooth, imperforate except for inconspicuous marginal pores. Basal pore chambers present. Ovicell hyperstomial, recumbent on succeeding zooid, spherical, with a large quadrate orifice, often developing a small umbo.

Remarks

H. spinigera is characterized by the small size of its zooids, the distinctive peristomial mucro and the closely grouped slender oral spines. Originally described fom the Loyalty Islands (Philipps 1899), it has since been reported from Hong Kong, the Philippines, and Sumbawa (Harmer 1957), and a single specimen was recorded from South Africa by O'Donoghue (1924), as *Mucronella serratilabris*. Some Australian Tertiary species such as *Mucronella mooraboolensis* MacGillivray (1895: 100, pl. 13 (fig. 9)) and *Rhynchopora spinifera* MacGillivray (1895: 102, pl. 13 (fig. 19)) may be related to *H. spinigera*.

Measurements (means of 10 values) in mm

Lz	lz
0,32	0,27

Hippoporella labiata sp. nov.

Fig. 19E–F

Material

Holotype: SAM–A26435, station SM 250, 31°59,3′S 29°22,5′E, 150–200 m.

Description

Colony encrusting. Zooids hexagonal, convex, small; separated by distinct grooves. Primary orifice lepralioid: anter longer than wide, with a finely denticulate edge, proximal border of poster gently concave; prominent, blunt lateral condyles present. Seven or eight short oral spines closely spaced around distal border of aperture. Frontal wall thick, vitreous, with a nodulated surface, imperforate except for indistinct marginal pores; a short cylindrical umbo developing just proximal to orifice and arching towards it. Avicularia adventitious, situated lateral to orifice, typically paired, mandible semi-elliptical, directed obliquely laterally; often replaced on one or both sides by a second type with an elongate, parallel-sided, distally-rounded mandible. Ovicell hyperstomial, pyriform, imperforate, with a distinct frontal labellum; becoming submerged in secondary calcification derived from distally succeeding zooids. Small basal pore chambers present.

Etymology

Labiatus (L.)—lipped, referring to the prominent suboral umbo.

Remarks

This species has a remarkable superficial resemblance to *H. multidentata* (Thornely), from Ceylon, described and figured by Harmer (1957: 1099, pl. 73 (figs 9–12)). Comparison of the present material with Thornely's type

specimen (BMNH 1906.12.3.4) shows several important differences. The orifice of *H. labiata* is proportionately less broad than in *H. multidentata*; the ovicell is longer and more distinctly pyriform than the rather squat ovicell of *H. multidentata*. Finally, the avicularia of *H. labiata* are very much larger than those of *H. multidentata* which, moreover, are consistently monomorphic. The systematic status of this species is considered at greater length on p. 104.

Measurements (means of 20 values) in mm

Lz	lz
0,45	0,39

Hippomenella Canu & Bassler, 1917

Hippomenella Canu & Bassler, 1917: 41. Brown, 1949: 513.

Hippomenella avicularis (Livingstone, 1926)

Fig. 19G

Lepralia tuberculata var. *avicularis* Livingstone, 1926: 93, pl. 5 (figs 1–3).
Hippomenella spatulata Harmer, 1957: 1095, pl. 72 (figs 27, 31).

Material

Stations SM 131, SM 163.

Description

Colony encrusting. Zooids large, oval, convex, separated by deep grooves. Primary orifice with a semi-orbicular anter separated from a narrower U shaped poster by prominent, blunt, basally deflected condyles. Orifice rim with six or seven spine bases. Frontal calcification thick and smooth, with numerous, very small inconspicuous pores; these are distributed around the periphery of the zooid, their frontal openings tend to shift centripetally as the frontal calcification thickens (giving a striated appearance to the wall), but the central area remains imperforate. Small adventitious avicularia present on all zooids, lateral to orifice and typically paired, mandible semi-elliptical, disto-laterally directed. Identical avicularia sporadically present frontally, up to five on a single zooid, orientation variable but directed away from the central area of the zooid. One or both of the lateral-oral pair may be replaced by an elongate avicularium with a slender spoon-like mandible. Small basal pore chambers present.

Remarks

This species was represented by several small dead colonies; ovicells were present but were so badly damaged that their structure could not be discerned.

Distribution

H. avicularis has been rarely reported and appears to be known from just three localities in the western Pacific (Harmer 1957).

Measurements (means of 16 values) in mm

Lz	lz
0,92	0,72

Family **Microporellidae** Hincks, 1879

Microporellidae Hinks, 1879: 156. Hayward & Ryland, 1979: 220.

Microporella Hincks, 1877

Microporella Hincks, 1877: 526. Hayward & Ryland, 1979: 220.

Microporella sp.

Fig. 20A

Material

Stations SM 163/164, SM 239.

Description

Colony encrusting. Zooids oval to hexagonal, broad, flat or slightly convex, separated by shallow grooves. Primary orifice subterminal, semicircular, with four or five short, distal oral spines. Frontal wall finely granular, perforated by numerous small pores; ascopore situated just proximal to orifice in distal third of zooid. Avicularium single, developed midway along the length of the zooid; mandible slender, setiform, up to 0,2 mm long, directed obliquely distally. No ovicells present.

Remarks

The familiar *Microporella ciliata* appears to have an almost cosmopolitan distribution, but the degree of morphological variation which it displays over its entire geographical range requires examination. The present material, consisting of two small colonies, is similar to *M. ciliata*, but in comparison with specimens from British waters appears rather larger, with more robust avicularian mandibles. No complete astogenetic series was represented in the *Meiring Naude* specimens, and neither colony possessed ovicells. consequently, the material is left unnamed until better specimens should be collected.

Measurements (means of 20 values) in mm

Lz	lz
0,57	0,42

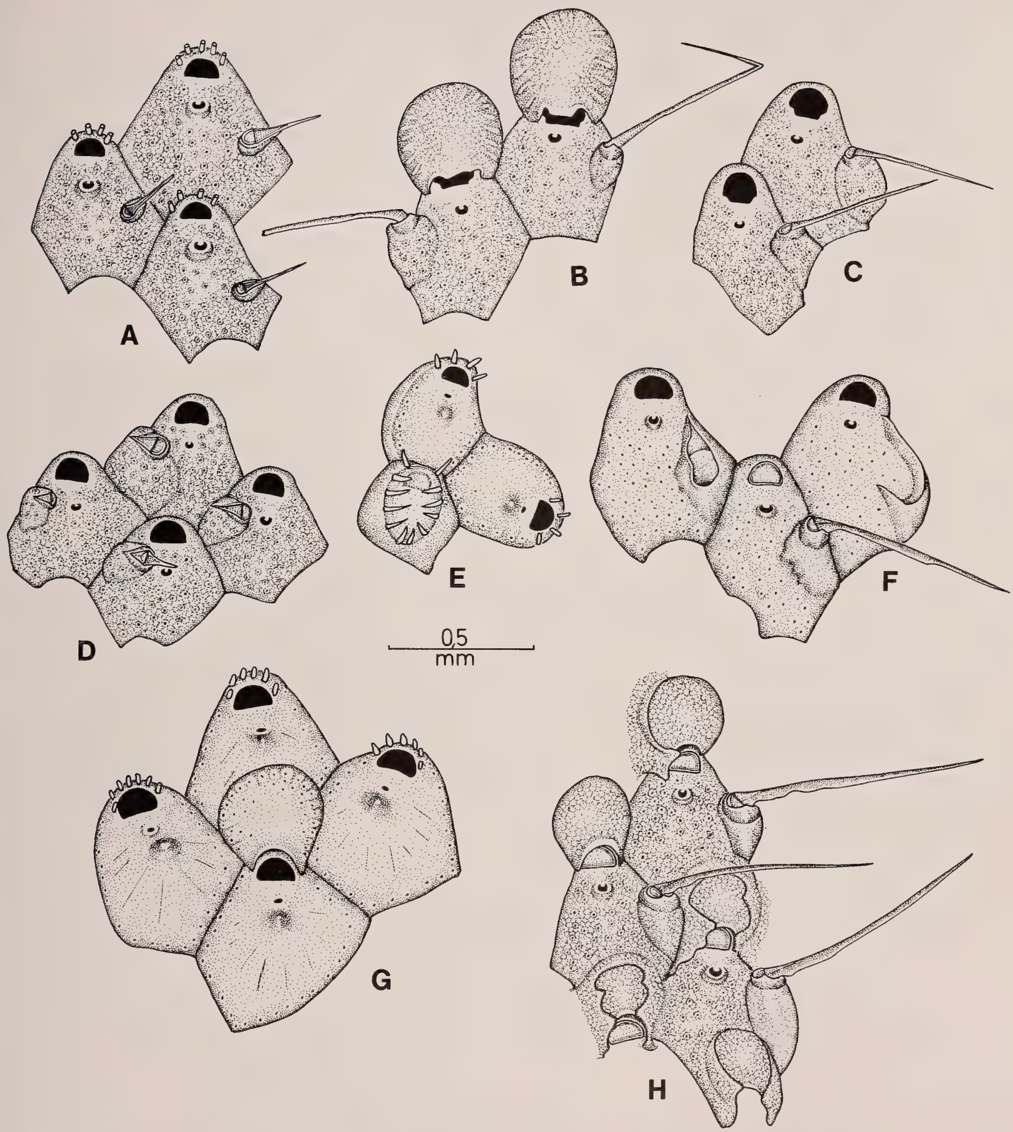

Fig. 20. A. *Microporella* sp. B–C. *Flustramorpha marginata* (Krauss). B. Ovicelled zooids. C. Young zooids, showing shape of primary orifice. D. *Flustramorpha flabellaris* (Busk). E. *Fenestrulina indigena* sp. nov., ancestrula and first two zooids. F. *Flustramorpha angusta* Hayward & Cook, young zooids showing shape of primary orifice. G. *Fenestrulina indigena* sp. nov., a group of zooids from close to the colony edge. H. *Flustramorpha angusta* Hayward & Cook, ovicelled zooids.

Flustramorpha Gray, 1872

Flustramorpha Gray, 1872: 168. Busk, 1884: 135.

All three species of *Flustramorpha* known from South Africa were present in the *Meiring Naude* samples. The genus is a homogenous one and the three species are often difficult to distinguish; it seems useful, therefore, to describe briefly the features considered here to be of importance. *F. flabellaris* (Busk) typically develops a tufted colony of short, broad lobes, but its most distinctive feature is the avicularium that, unlike those of the other two species, has a short acuminate mandible, and a palate that is almost parallel to the frontal plane of the zooid. In *F. marginata* (Krauss) and *F. angusta* Hayward & Cook the avicularium has a setiform mandible, and the palate is orientated at an oblique, or even perpendicular, angle to the frontal plane.

The avicularian mandibles of *F. angusta* were not preserved in the type specimen. They are similar to those of *F. marginata*, setiform and up to 0,75 mm long; they are broadened basally close to the point of articulation (Fig. 20H). The ovicell of *F. angusta* is proportionately smaller, narrower and more depressed than that of *F. marginata*, its width being considerably less than that of the maternal zooid. Further, whereas in *F. marginata* the ovicell is prominent at all stages of growth, in *F. angusta* it is progressively obscured by secondary calcification which typically overhangs its aperture on each side. The orifice of *F. angusta* is semi-elliptical, with a straight proximal border (Fig. 20F), whereas that of *F. marginata* has distinct lateral condyles that impart to it a characteristic outline at all ontogenetic stages (Fig. 20C).

Finally, it may be the case that the colony form of these latter two species are a further useful specific character. The specimens of *F. angusta* were all slender, unbranched, strap-like colonies, up to 50 mm long, with a maximum width of 3,5 mm. The material of *F. marginata* was mostly fragmentary, but included two regularly bifurcating colonies, 30 mm and 40 mm high, with a maximum branch width of 4 mm.

Flustramorpha flabellaris (Busk, 1854)

Fig. 20D

Eschara flabellaris Busk, 1854: 91, pl. 107 (figs 7–10).
Microporella flabellaris: Marcus, 1922: 28, fig. 16.

Material

Stations SM 179, SM 180.

Flustramorpha marginata (Krauss, 1837)

Fig. 20B–C

Flustra marginata Krauss, 1837: 35, fig. 3.
Flustramorpha marginata: Busk, 1884: 135, pl. 20 (fig. 8). Hayward & Cook, 1979: 80.

Material

Stations SM 163/164, SM 184, SM 185, SM 239.

Flustramorpha angusta Hayward & Cook, 1979

Fig. 20F, H

Flustramorpha angusta Hayward & Cook, 1979: 80, fig. 11E.

Material

Stations SM 131, SM 163, SM 163/164, SM 184, SM 185.

Fenestrulina Jullien, 1888

Fenestrulina Jullien, 1888: 37. Hayward & Ryland, 1979: 224.

Fenestrulina indigena sp. nov.

Fig. 20E–G

Material

Holotype: SAM–A26436, station SM 163, 33°04,6′S 28°06,6′E, 90 m.
Other material: station SM 163/164.

Description

Colony encrusting. Zooids oval to hexagonal, convex, separated by distinct grooves. Primary orifice semicircular, with a thin raised rim, relatively small—constituting less than one-tenth of the total zooid length; six or seven short distal oral spines present. Frontal wall thin and hyaline, with a few radiating sutures; marginal pores distributed in a single series, small and rather inconspicuous. Ascopore situated just proximal to orifice in the distal half of the zooid, small, transversely oval; a short umbo develops proximal to the ascopore but does not support it. Ovicell recumbent on succeeding zooid, globular, as wide as long; smooth surfaced, with faint marginal flutings. Ancestrula tatiform, oval, 0,32 mm long, with twelve marginal spines.

Etymology

Indigenus (L.)—native to.

Remarks

Fenestrulina indigena may be distinguished from other species of the genus by the number of oral spines, and by the characteristic frontal umbo, which does not seem to be in any way associated with the ascopore.

Measurements (means of 20 values) in mm

Lz	lz
0,60	0,43

Family **Hippothoidae** Levinsen, 1909

Hippothoidae Levinsen, 1909: 274. Hayward & Ryland, 1979: 246.

Trypostega Levinsen, 1909

Trypostega Levinsen, 1909: 280. Hayward & Ryland, 1979: 258.

Trypostega venusta (Norman, 1864)

Lepralia venusta Norman, 1864: 84, pl. 10 (figs 2–3).
Trypostega venusta: Hayward & Ryland, 1979: 258, fig. 111.

Material

Stations SM 163, SM 163/164, SM 164, SM 239.

Distribution

Trypostega venusta has a circumtropical, warm-temperate distribution. It has been reported from the Red Sea, Mauritius, and east Africa (Harmer 1957) but has not been recorded before from South Africa.

Family **Gigantoporidae** Bassler, 1935

Gigantoporidae Bassler, 1935: 32. Harmer, 1957: 878.

Gigantopora Ridley, 1881.

Gigantopora Ridley, 1881: 47. Harmer, 1957: 879.

Gigantopora polymorpha (Busk, 1884)

Gephyrophora polymorpha Busk, 1884: 167, pl. 34 (fig. 2).
Adeonella ponticula O'Donoghue, 1924: 54, pl. 4 (fig. 23).
Gigantopora polymorpha: Brown, 1952: 208, figs 145–146. Hayward & Cook, 1979: 81.

Material

Stations SM 179, SM 180, SM 185.

Remarks

Numerous live colonies of this characteristically South African species were collected at stations SM 179 and SM 185.

Gigantopora foraminosa sp. nov.

Fig. 11E–F

Material

Holotype: SAM–A26437, station SM 163/164, 33°04,6′S 28°06,6′E, 90 m.
Other material: stations SM 131, SM 163, SM 163/164, SM 164, SM 184.

Description

Colony erect, rigid, cylindrical, branching irregularly; attached by an encrusting base, up to 21 mm high in present material, the branches broadening

distally. Zooids in alternating longitudinal series, disposed all around the branch axis; rectangular, flat or slightly convex, separated by distinct raised sutures. Primary orifice longer than wide; anter D-shaped, poster concave, constituting a broad, shallow, U-shaped sinus between small lateral condyles. Frontal wall closely perforated by numerous round pores, each in a distinct pit. Peristomial complex occupying distal half of zooid; initiated by the development of paired lateral oral avicularia with elongate, acute triangular rostra, directed medially. These arch over the primary orifice and fuse medially; proximal to the area of fusion, a transversely oval spiramen communicates with the space above the primary orifice, distally a rim of calcification delimits a semicircular secondary orifice. Border of secondary orifice frequently peaked medially on either or both the distal and proximal edge. The gap between the two avicularian cystids is infilled as the opening of the spiramen is elaborated; this develops a lobed distal hood, above which two further lacunae are seen, separated medially by a longitudinal ridge. In later ontogenetic stages these lacunae are completely obliterated. Ovicell large, prominent but partially immersed; broadly oval and densely punctured by small pores, becoming rather rugose. Secondary orifices of ovicellate zooids broader than those of non-ovicellate zooids. Vertical walls of zooids with large and distinct multiporous septula.

Etymology

Foraminosus (L.)—full of holes.

Remarks

This species is distinguished from *G. polymorpha* by its generally larger dimensions, by its relatively longer primary orifice, and by the characteristic twinned lacunae below the oral avicularia. A similar fossil species, *Porina cribraria*, was described from the Australian Tertiary by MacGillivray (1895: 104, pl. 14 (fig. 25)).

Measurements (mean values) in mm

Zooids			Ovicell		
n	Lz	lz	n	Lov	lov
25	1,07	0,6	8	0,48	0,66

Family **Adeonellidae** Gregory, 1893

Adeonellidae Gregory, 1893: 241. Cook, 1973: 246.

Adeonella Busk, 1884

Adeonella Busk, 1884: 183. Cook, 1968: 180.

The genus *Adeonella* is abundantly represented in eastern South African waters and a total of 15 species may now be recognized. *A. regularis* (Busk,

1884) seems to have been the first species to be described from this area; the type specimen is no longer extant, however, and the status of this species remains to be clarified. Similarly, *A. pygmaea* Levinsen (1909), the identity of which even Levinsen was uncertain about, has not been reported since the original, rather brief account. O'Donoghue (1924) described four new species of *Adeonella* from South Africa; *A. coralliformis*, *A. expansa*, and *A. ligulata* are well-defined species, the type specimens of which have been examined during the preparation of this account. *A. ponticula* O'Donoghue (1924) has proved to be identifiable with *Gigantopora polymorpha* (Busk) (Hayward & Cook 1979); *A. pectinata* Busk, described from a single specimen collected by the *Challenger* off Cape York, Queensland, was reported by O'Donoghue (1924) from two South African localities but his specimens prove to represent *A. gibba* sp. nov. *Adeonella meandrina* O'Donoghue & De Watteville (1944) has been shown (Cook 1973) to be referable to the umbonuloid genus *Adeonellopsis*, and *A. jellyae* Levinsen (1909) may be assigned to *Laminopora* Michelin, 1842 (Cook 1983*a*).

The first *Meiring Naude* collections included two undescribed species of *Adeonella*, *A. majuscula* and *A. cracens* (Hayward & Cook 1979). *A. falcicula* and *A. cultrata* were then described (Hayward 1981) from South African specimens collected by the *Galathea* deep-sea expedition. The present collections yielded eight new species of *Adeonella*, and it would seem useful at this stage to present a key to the presently known South African species of the genus. The morphological features of most use in distinguishing between the different species are: the shape of the primary orifice, the shape and position of the spiramen, the size, orientation, and position, relative to the secondary orifice, of the peristomial avicularia. Certain later ontogenetic features seem to be consistent in some species, and the form of the colony may prove also to be an important character.

PROVISIONAL KEY TO THE SOUTH AFRICAN SPECIES OF *ADEONELLA*

1. Primary orifice orbicular, oval or quadrate, without a sinus 2
— Primary orifice with a distinct sinus 6

2. Primary orifice longer than broad, quadrate. Spiramen broadly oval, developing a proximal concavity in later ontogeny; flanked by one or two small medially directed avicularia. Other avicularia rare. Marginal vicarious avicularia absent
A. infirmata sp. nov.
— Primary orifice oval or rounded. No concavity proximal to spiramen 3

3. Primary orifice almost circular. Spiramen oval, situated close to distal end of peristome, flanked by small paired medially directed avicularia, a second pair often present on distal rim of peristome. Marginal vicarious avicularia absent
A. falcicula Hayward (1981)
— Primary orifice transversely oval. Spiramen flanked by paired or single avicularia. Enlarged vicarious avicularia present on colony margins 4

4. Spiramen distinctly oblong, its primary outline contrasting with, and visible beneath, the rounded opening developed in later ontogeny. Small paired avicularia developed lateral to spiramen, extending distally towards, but not reaching the proximal border of the secondary orifice .... *A. cracens* Hayward & Cook (1979)
— Spiramen round or oval at all ontogenetic stages 5

5. Spiramen large, round; situated in the middle of the zooid, well proximal to the secondary orifice. A single avicularium present in early ontogeny, elongate, extending obliquely medially, between the spiramen and the secondary orifice. Smaller frontal avicularia abundant in later ontogenetic stages ..... *A. majuscula* Hayward & Cook (1979)

— Spiramen large, oval; situated in distal half of zooid, close to base of peristomial calcification. A single frontal avicularium developed just proximal to spiramen, extending obliquely distally towards, and almost reaching, the proximal border of the secondary orifice. Other frontal avicularia apparently absent ... *A. cultrata* Hayward (1981)

6. Spiramen, in *early* ontogenetic stages, overarched from one side by a distinct hood, so that the plane of its aperture is perpendicular to the frontal plane of the zooid. A small distally directed avicularium adjacent to spiramen 7

— Spiramen, in *early* ontogenetic stages, with a low distal arch, and frequently with a distinct concavity proximal to it, or normal to frontal plane, but without a laterally developed hood 9

7. Primary orifice as broad as, or broader than long. A single, median, proximally directed avicularium developing proximal to, and partly obscuring, the spiramen in later ontogeny. Colony forming slender blades .... *A. gibba* sp. nov.

— Primary orifice longer than broad. No median, proximally directed avicularium .. 8

8. Sinus of primary orifice forming a short symmetrical U. Small avicularia frequent on frontal wall and around peristome in later ontogeny. Colony forming slender blades *A. abdita* sp. nov.

— Sinus of primary orifice forming a broad, shallow U. Small avicularia infrequent in later ontogeny; typically one extending obliquely between spiramen and secondary orifice, and one orientated transversely along proximal border of secondary spiramen. Colony forming broad, flat plates...................... *A. expansa* O'Donoghue (1924)

9. Spiramen large, oval or circular, with the sinus visible through it in at least the earliest ontogenetic stages 10

— Spiramen small, circular, sinus not visible 14

10. Primary orifice with slender, pointed sinus. A single, median, proximally directed avicularium developed proximal to the spiramen in later ontogeny. Colony forming short, broad plates .... *A. alia* sp. nov.

— Primary orifice with a V- or U-shaped sinus. Colony typically forming slender blades .. 11

11. Sinus narrow, parallel-sided. Peristomial avicularia typically paired, arising distal to spiramen and extending medially above distal border of secondary orifice *A. decipiens* sp. nov.

— Sinus forming a symmetrical, broader U-shape. Peristomial avicularia single or paired 12

12. Primary orifice broader than long. Peristomial avicularium single, short; situated adjacent to spiramen, extending obliquely distally towards proximal border of secondary orifice .... *A. conspicua* sp. nov.

— Primary orifice as long as, or longer than broad. Peristomial avicularia typically paired 13

13. Peristomial avicularia paired, arising distal to spiramen and directed medially, the apices of the rostra almost converging distal to the secondary orifice. Frontal wall convex proximal to spiramen .... *A. coralliformis* O'Donoghue (1924)

— Peristomial avicularia paired, arising adjacent to, or just distal to the spiramen and directed medially, extending between the spiramen and the proximal border of the secondary orifice. Frontal wall concave proximal to spiramen; later filled by a proximally directed avicularium .... *A. confusanea* sp. nov.

14. Primary orifice as broad as long, anter and poster of almost equal length. Spiramen situated in distal half of zooid but distant from the proximal border of the secondary orifice .... *A. distincta* sp. nov.

— Primary orifice much broader than long; poster very shallow, constituting less than one-third of orifice length. Spiramen small, situated close to proximal border of secondary orifice .... *A. ligulata* O'Donoghue (1924)

Adeonella majuscula Hayward & Cook, 1979

Adeonella majuscula Hayward & Cook, 1979: 82, fig. 10E–H.

Material

Station SM 233.

Remarks

Part of a single large colony, 75 mm high, was collected from a depth of 540–80 m.

Adeonella cracens Hayward & Cook, 1979

Adeonella cracens Hayward & Cook, 1979: 85, fig. 10I–L. Hayward, 1981: 44, Fig. 22A.

Material

Station SM 103.

Remarks

Dead fragments only were recovered from the above station.

Adeonella decipiens sp. nov.

Fig. 21A–E

Material

Holotype: SAM–A26438, station SM 163, 33°04,6′S 28°06,6′E, 90 m.

Other material: stations SM 131, SM 163/164, SM 179, SM 180, SM 184, SM 185.

Description

Colony erect, branching, rigid; branches bilaminar, slender, up to 5 mm wide. Zooids oval to hexagonal, broadening distally, tapered proximally, separated by indistinct grooves which are increasingly obscured in older zooids. Primary orifice semi-orbicular, sinus slender, U-shaped; peristome thickened, prominent, tending to project from branch surface; inner proximal edge with a blunt projecting knob (Fig. 21B), later hidden as secondary calcification progresses, secondary orifice eventually orbicular. Frontal wall convex, finely granular, with numerous small pores, indistinct in newly developed zooids, more pronounced in later ontogenetic stages. Spiramen oval and large, situated at base of peristome so that calcification between it and the secondary orifice forms merely a slender bridge in young zooids; despite further thickening, the proximal border of the primary orifice is visible in all but the most heavily calcified zooids. Adventitious avicularia paired, lateral to the orifice, rostrum acute triangular, directed distomedially along the distal border of the secondary orifice. In later ontogenetic stages these avicularia may be obliterated and replaced by a second generation with a similar orientation, or more proximally

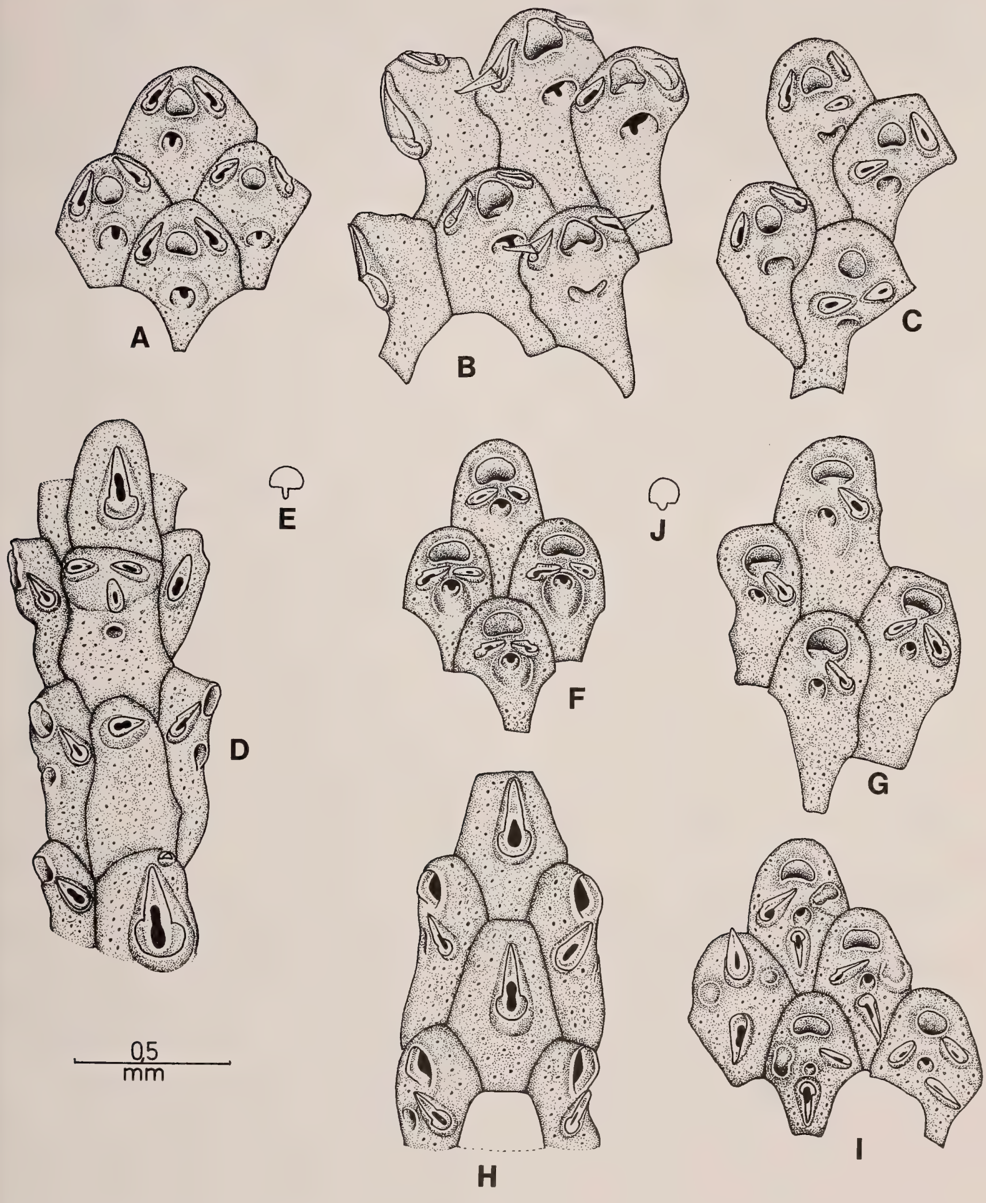

Fig. 21. A–E. *Adeonella decipiens* sp. nov. A. Four typical zooids. B. Zooids from a growing edge, showing characteristic shape of early peristome. C. Older zooids with hooded spiramina. D. View of a branch edge, showing vicarious and adventitious avicularia. E. Outline diagram of primary orifice. F–J. *Adeonella confusanea* sp. nov. F. Young zooids, with concave frontal walls. G. Later zooids, with thickened frontal walls. H. View of a branch edge, with vicarious avicularia. I. Zooids from near the base of the colony, with secondarily developed frontal avicularia. J. Outline diagram of primary orifice.

situated with the rostra extending between the spiramen and the proximal border of the secondary orifice; rarely, the avicularia may be developed frontally, proximal to the spiramen. Vicarious avicularia developed along the branch edge, with enlarged, distally directed rostra, interspersed with what may be small kenozooids, or autozooids with obliterated orifices; both these and the vicarious avicularia may bear small adventitious avicularia.

Etymology

Decipia (L.)—deception, a reference to the similarity between this species and *A. coralliformis*.

Remarks

At the distal tips of branches the peristomes and avicularia project markedly from the surface. With continued calcification both are progressively immersed, the spiramen becomes deeply sunk, more rounded and smaller. *A. decipiens* is superficially similar to *A. coralliformis* O'Donoghue but is readily distinguished by the small size of its zooids and by the primary orifice, which is almost circular in *A. coralliformis*. The material included numerous living and dead fragments, up to 22 mm long.

Measurements (means of 25 values) in mm

Lz	lz
0,50	0,36

Adeonella confusanea sp. nov.

Fig. 21F–J

Material

Holotype: SAM–A26439, station SM 185, 33°39,3′S 27°11,6′E, 90 m.
Other material: stations SM 163, SM 163/164, SM 179, SM 185.

Description

Colony erect, branching, rigid, attached by an encrusting base; branches bilaminar, up to 39 mm long in present material, with a maximum width of 4 mm. Zooids oval to rectangular, hexagonal in central part of branch, convex, separated by deep grooves. Primary orifice semi-orbicular, with a short U-shaped sinus; peristome with a broad blunt denticle within proximal border, visible in earlier ontogenetic stages, developing a transversely oval secondary orifice. Avicularia typically paired, occasionally single, arising lateral to spiramen, rostrum acute triangular, directed distomedially between spiramen and secondary orifice, close to the proximal border of the latter. Frontal wall granular, convex and rather rugose, with numerous small pores; spiramen circular, situated close to proximal base of peristome, sinus visible through it in

youngest zooids. Later in ontogeny, additional avicularia may be developed elsewhere on the frontal wall; most frequently, a single avicularium is developed medially, proximal to spiramen. Proximally directed vicarious avicularia present in a single linear series along the branch edge.

Etymology

Confusaneus (L.)—mixed, referring to characters shared with other species (below).

Remarks

The proximally directed frontal avicularium, which develops in later ontogenetic stages, is also seen in *A. abdita* (p. 97). However, that species may be distinguished from *A. confusanea* by the shape of the primary orifice (Fig. 23D), and by the broad, flat, plate-like branches of the colony.

Measurements (means of 25 values) in mm

Lz	lz
0,48	0,27

Adeonella conspicua sp. nov.

Fig. 22A–D

Material

Holotype: SAM–A26440, station SM 179, 33°30,3′S 27°22,1′E, 80 m.

Description

Colony erect, branching, rigid. Zooids oval to hexagonal, or irregular, separated by distinct grooves. Primary orifice almost semicircular, with a short, wide and shallow sinus. Peristome thickened, nodular, but relatively depressed, secondary orifice semicircular. Frontal wall convex, nodular, with small but distinct pores; spiramen circular, situated close to base of peristome. Sinus of primary orifice visible through it in newly developed zooids. Avicularia typically single, rarely paired, situated lateral to spiramen; rostrum triangular, relatively short, at an acute angle to frontal plane, directed distomedially or, rarely, proximally. In zooids towards the basal region of the colony, avicularia may be developed elsewhere on the frontal wall. Marginal vicarious avicularia very characteristic, rostrum hooked and projecting from the edge of the branch; interspersed with smaller types, or bearing them.

Etymology

Conspicuus (L.)—manifest, referring to the characters of the species.

Remarks

A single juvenile colony was found, 9 mm high and bearing three short lobes with a maximum width of 2 mm. Despite this shortage of material, the

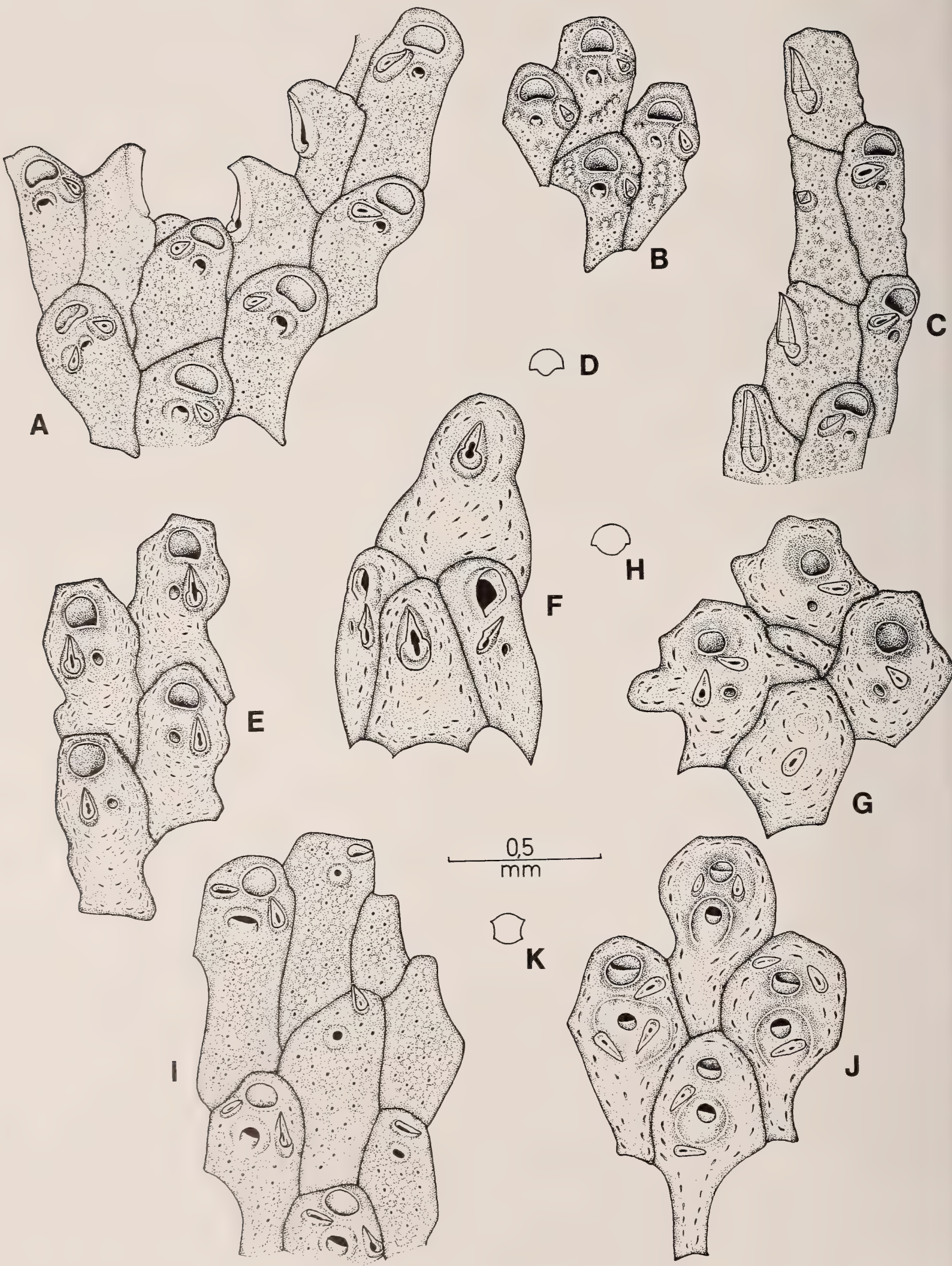

Fig. 22. A–D. *Adeonella conspicua* sp. nov. A. Young zooids at a branch bifurcation, note prominent hooked avicularian rostra. B. Older zooids with nodular frontal walls. C. The branch edge, with vicarious avicularia. D. Outline diagram of primary orifice. E–H. *Adeonella distincta* sp. nov. E. Four typical zooids. F. The branch edge, with vicarious avicularia. G. Old zooids from the colony base. H. Outline diagram of primary orifice. I–K. *Adeonella infirmata* sp. nov. I. Young zooids from close to the colony margin, note kenozooids on right. J. Old zooids with thickened frontal walls. K. Outline diagram of primary orifice.

specimen seems sufficiently distinctive to warrant the introduction of a new specific name.

Measurements (means of 25 values) in mm

Lz	lz
0,47	0,25

Adeonella distincta sp. nov.

Fig. 22E–H

Material

Holotype: SAM–A26441, station SM 185, 33°39,3′S 27°11,6′E, 90 m.

Description

Colony erect, branching, rigid, attached by encrusting base; branches bilaminar, slender, up to 35 mm long in present material, with a maximum width of 2 mm. All branches in the same plane. Zooids elongate, rectangular, separated by deep grooves, becoming irregular in outline in later ontogeny. Primary orifice broadly drop-shaped: anter semicircular, poster forming a broad and symmetrical U-shape. Peristome developing an orbicular secondary orifice. Avicularium single or, rarely, paired, situated lateral to spiramen and directed distally; rostrum acute triangular, not quite reaching the proximal border of the secondary orifice. Frontal wall convex, finely granular, with numerous small pores; spiramen more or less centrally placed, midway along the length of the zooid, at first longitudinally oval, becoming quite circular as frontal calcification thickens. Vicarious avicularia developed along branch edges, interspersed with small kenozooids, which may or may not bear small adventitious avicularia.

Etymology

Distinctus (L.)—different.

Remarks

The orientation of the frontal avicularium may vary within the colony, and in some zooids the rostrum may extend medially between the spiramen and the secondary orifice. In the oldest parts of the colony avicularia may be developed proximal to the spiramen, but there are rarely more than three per zooid. This species is most similar to *A. cracens* Hayward & Cook (1979) but is distinguished by the smaller size of its zooids and by the shape of the primary orifice, which in *A. distincta* is sinuate but in *A. cracens* forms a simple transverse ellipse. Fragments of three live colonies of this species were collected.

Measurements (means of 25 values) in mm

Lz	lz
0,59	0,30

Adeonella infirmata sp. nov.

Fig. 22I–K

Material

Holotype: SAM–A26442, station SM 239, 32°14,8′S 29°00,8′E, 90 m.

Description

Colony erect, branching, rigid, attached by an encrusting base; branches bilaminar, up to 45 mm high in present material, with a maximum width of 5 mm. Zooids elongate, hexagonal or rectangular, rounded distally and often tapered proximally; smallest zooids in middle region of branch. Primary orifice bell-shaped, proximal border shallowly convex below indistinct condyles. Peristome with orbicular secondary orifice. Avicularium single or paired, arising laterally at a level midway between the spiramen and the secondary orifice; rostrum acute triangular, short, directed distally or distomedially, typically extending to proximolateral corners of secondary orifice. Frontal wall convex, finely granular, evenly perforated by numerous small pores; spiramen situated close to proximal border of secondary orifice, large, transversely oval, arched, the proximal border of the primary orifice visible in all but the most heavily calcified zooids. Small adventitious avicularia may develop elsewhere on the frontal wall in the later stages of ontogeny, with variable orientation. Vicarious avicularia present in single linear series along branch edge, the rostra of which frequently project noticeably from the branch edge. These may alternate with small kenozooids.

Etymology

Infirmis (L.)—weak, referring to the rather delicate form of the colony.

Remarks

Zooid rows frequently terminate at the edges of the branch in small kenozooids which often bear adventitious avicularia. The longitudinal branch keel typical of some of the species described here (p. 99) is only poorly developed in *A. infirmata*; it seems to be formed from thickened frontal calcification rather than from inflated avicularian cystids, although small adventitious avicularia are more frequent in the middle regions of the branch. Fragments of five living colonies were collected.

Measurements (means of 25 values) in mm

Lz	lz
0,71	0,30

Adeonella abdita sp. nov.

Fig. 23A–E

Material

Holotype: SAM–A26443, station SM 239, 32°14,8′S 29°00,8′E, 90 m.
Other material: stations SM 163, SM 163/164, SM 164, SM 185.

Description

Colony erect, branching, rigid, attached by an encrusting base; branches bilaminar, up to 30 mm long in present material, with a maximum width of 5 mm. Zooids elongate, rectangular or oval, frequently tapered proximally; separated by distinct grooves, becoming obscured in older parts of colony. Primary orifice as wide as long, with inconspicuous, blunt lateral condyles demarcating a broad, shallow proximal sinus. Peristome with a transversely oval secondary orifice, the inner proximal edge developing a blunt denticle. Frontal wall convex, granular, closely punctured by numerous small pores. Spiramen medially situated in the distal third of the zooid, orbicular, oval or elongate, overarched from the left or right by a distinct hood, so that its opening appears to be perpendicular to the frontal plane of the zooid. A single avicularium adjacent to spiramen, rostrum acute triangular, directed distally; becoming quite immersed, below the level of the spiramen hood. A second avicularium may be developed on the other side of the spiramen, preventing complete development of its hood; occurs rarely in some colonies, more frequently in others. Additional avicularia may develop laterally, between the spiramen and the secondary orifice, smaller than the frontal type, single or paired, with rostrum directed towards the peristome. In the oldest parts of the colony these may be very frequent, with four or five developed around the distal end of the zooid, all directed towards the peristome. Frontal avicularia are progressively immersed and eventually completely obscured; peristomial avicularia then proliferate, but there is no regeneration of regularly orientated frontal avicularia (cf. *A. gibba*, p. 99).

In well-grown colonies each branch has a median longitudinal keel, formed by the development of numerous adventitious avicularia, each with a particularly voluminous cystid. Large vicarious avicularia present in single linear series along branch edges.

Etymology

Abditus (L.)—hidden, referring to the spiramen.

Remarks

Adeonella expansa O'Donoghue shows a similar development of the spiramen to that of *A. abdita*, but differs in that the adjacent avicularium is very small, being scarcely longer than the spiramen itself. Further, unlike the present species, the peristomial avicularia are almost medially situated, with

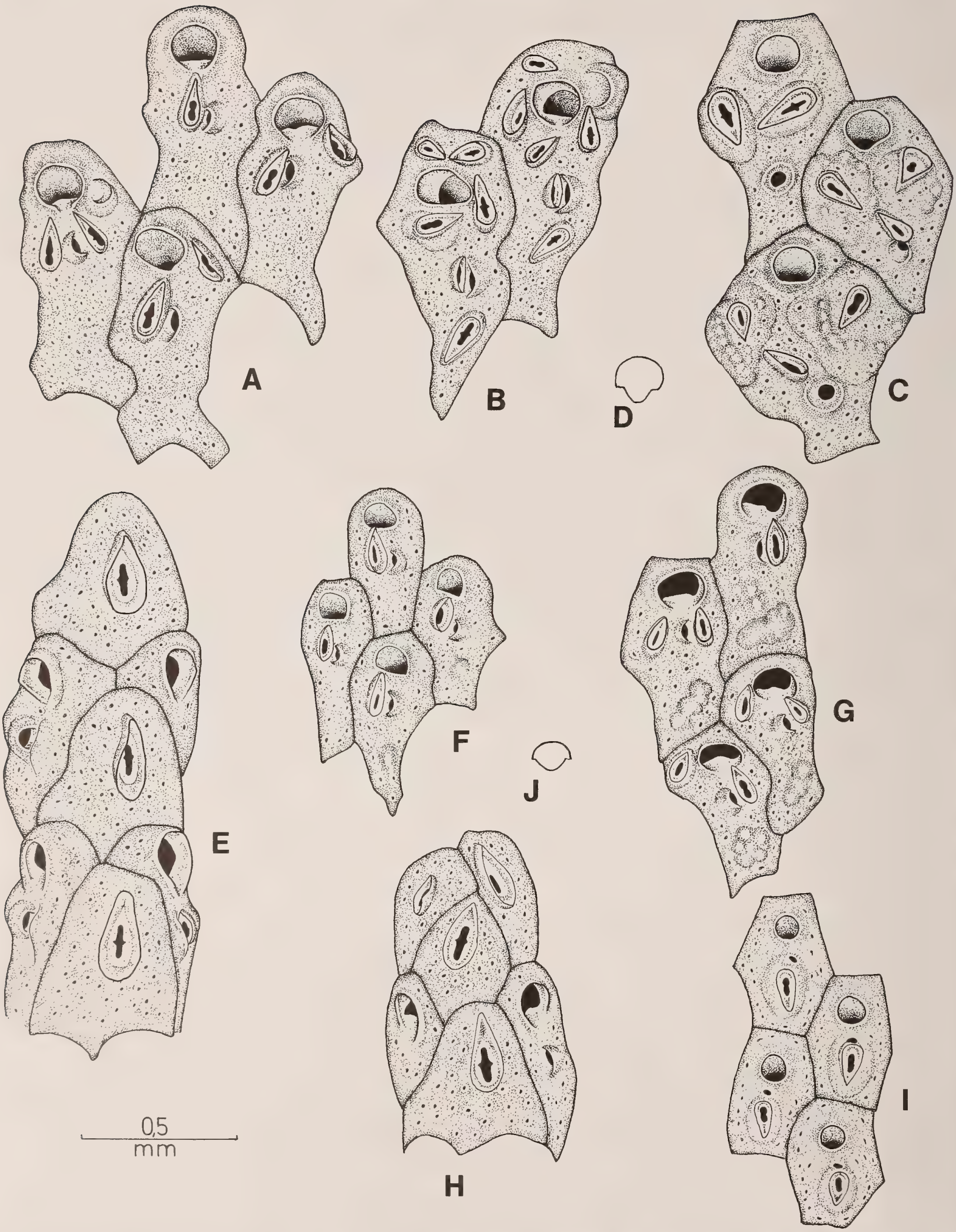

Fig. 23. A–E. *Adeonella abdita* sp. nov. A. Young zooids showing characteristic form of spiramen and adjacent avicularium. B. Older zooids, with numerous additional avicularia. C. Zooids from the branch keel, showing immersed spiramina and prominent avicularian cystids. D. Outline diagram of primary orifice. E. View of the branch edge, showing vicarious avicularia. F–J. *Adeonella gibba* sp. nov. F. Young zooids showing characteristic form of spiramen and adjacent avicularium. G. Later zooids with nodular frontal walls. H. The branch edge showing vicarious avicularia. I. Old zooids from the colony base, with proximally directed frontal avicularia. J. Outline diagram of primary orifice.

transversely orientated mandibles. The colony of *A. expansa* develops broad plate-like branches.

Measurements (means of 25 values) in mm

Lz	lz
0,76	0,34

Adeonella gibba sp. nov.

Fig. 23F–J

Adeonella pectinata: O'Donoghue, 1924: 51.

Material

Holotype: SAM–A26444, station SM 179, 33°30,3′S 27°22,1′E, 80 m.
Other material: stations SM 163, SM 163/164, SM 179, SM 180, SM 185.

Description

Colony erect, branching, rigid, rising from an encrusting base; branches bilaminar, up to 4 mm wide. Zooids oval to rectangular, convex; separated by deep grooves, less apparent in oldest parts of colony. Primary orifice as wide as long, proximal half constituting a broad shallow sinus. Peristome with an orbicular secondary orifice, inner proximal border with a broad shelf-like denticle. Frontal wall granular, closely perforated by numerous round pores which become accentuated as calcification continues; marginal series particularly prominent in later ontogenetic stages. A pronounced umbo frequently present on proximal frontal wall. Spiramen medially situated in distal half of zooid; relatively large and rather elongate, partly hidden by a lateral hood, the aperture thus appearing perpendicular to frontal plane of zooid. A single lateral avicularium developed, sporadically, just proximal to aperture, rostrum extending obliquely distally on to the peristome; frequently absent. Larger, vicarious, avicularia present in single linear series along branch edges, and often intercalated in zooid rows at the margins of the branch; mandible acute triangular, distally directed.

As secondary calcification proceeds the spiramen becomes deeply immersed, and the frontal wall quite concave; a second frontal avicularium is then budded, obscuring the first and partly filling the concavity. This new avicularium is orientated proximally in all zooids; the extended opening of the spiramen is just visible at its distal end. A median longitudinal ridge may be apparent along the branches of the oldest part of the colony, formed by the development of extra adventitious avicularia; elsewhere, however, the avicularia do not proliferate as they do in *A. abdita* (above).

Etymology

Gibbus (L.)—protuberant, referring to the frontal umbones of later zooids.

Remarks

The secondary frontal avicularium, with its constant orientation, is a characteristic feature of this species and serves to distinguish it further from *Adeonella abdita*.

Measurements (means of 25 values) in mm

Lz	lz
0,52	0,29

Adeonella alia sp. nov.

Fig. 24A–D

Material

Holotype: SAM–A26445, station SM 179, 33°30,3′S 27°22,1′E, 80 m.

Description

Colony erect, branching, rigid, attached by an encrusting base; branches bilaminar, broad and flat with lobed edges, up to 20 mm wide. Zooids rounded distally, tapered proximally. Primary orifice with semicircular anter and slender V-shaped poster, condyles strongly marked. Peristome with a semicircular or semi-elliptical secondary orifice, the inner proximal border thickened and raised medially to form a broad denticle with a serrated margin. Spiramen situated close to base of peristome, its orifice vertical to frontal plane of zooid; proximal edge incomplete in younger zooids, later quite rounded. Frontal wall finely granular, with large, deeply sunk pores giving it a rugose appearance. Avicularium single or paired, arising adjacent to spiramen, elongate rostrum directed distomedially towards the proximal border of the secondary orifice. When only a single avicularium is present a short conical umbo may be developed on the opposite side of the spiramen. In early ontogeny the middle area of the frontal wall, proximal to the spiramen, is deeply concave; subsequently an extra adventitious avicularium develops here, with a prominent tumid umbo and an elongate, proximally directed rostrum. Other, smaller, avicularia may develop elsewhere on the frontal surface, and along the branch edges, in the oldest parts of the colony.

Etymology

Alius (L.)—another.

Remarks

The single colony found was 40 mm high, with broad lobed branches; either flat, or concave, or distinctly twisted about the longitudinal axis. The concave frontal wall, and the subsequent development of a proximally directed avicularium, recall the morphology of *A. gibba* (above). However, *A. alia* is

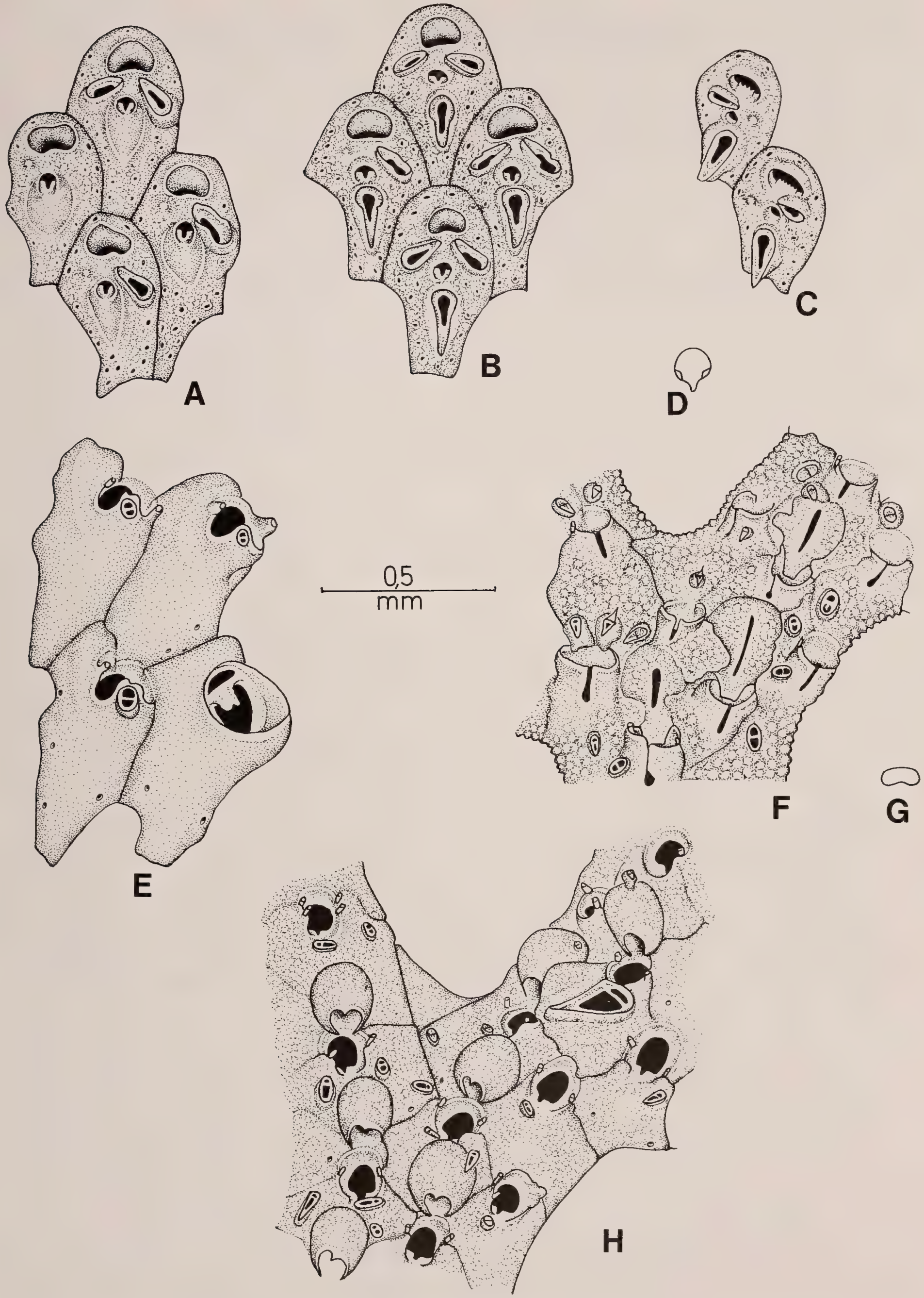

Fig. 24. **A–D.** *Adeonella alia* sp. nov. A. Young zooids, with typical concave frontal walls. B. Later zooids, with characteristic development of frontal avicularia. C. Two zooids in oblique view to show peristomial denticle. D. Outline diagram of primary orifice. E. *Reteporella dinotorhynchus* Hayward & Cook. F–G. *Sertella lata* (Busk). F. Portion of a colony showing ovicelled zooids. G. Outline diagram of primary orifice. H. *Schizoretepora tessellata* (Hincks).

distinguished from that species by the shape of the primary orifice, the form of the spiramen, and by the characteristic form of its colony.

Measurements (means of 20 values) in mm

Lz	lz
0,52	0,29

Family **Tessaradomidae** Jullien, 1903

Tessaradomidae Jullien *in* Jullien & Calvet, 1903: pl. 14. Hayward & Ryland, 1979: 242.

Tessaradoma Norman, 1869

Tessaradoma Norman, 1869: 309. Lagaaij & Cook, 1973: 494. Hayward & Ryland, 1979: 242.

Tessaradoma bispiramina Hayward & Cook, 1979

Tessaradoma bispiramina Hayward & Cook, 1979: 90, fig. 13A–D.

Material

Stations SM 103, SM 151, SM 233, SM 234.

Remarks

Living colonies were collected from stations SM 233 and SM 234, within the bathymetric range observed by Hayward & Cook (1979).

Tessaradoma circella Hayward & Cook, 1979

Tessaradoma circella Hayward & Cook, 1979: 91, fig. 13E–H. Hayward 1981: 48, fig. 25.

Material

Stations SM 103, SM 233.

Remarks

The astogeny of the basal attachment ring of *Tessaradoma circella* and the morphology of the ancestrula have recently been described by Hayward (1981).

Family **Sertellidae** Jullien, 1903

Sertellidae Jullien *in* Jullien & Calvet, 1903: 57. Hayward & Ryland, 1979: 260.

The genera and species here assigned to the Sertellidae do not, perhaps, constitute a natural assemblage, yet display a confusing similarity in many of their morphological features. Lagaaij (1952: 109–110) followed accepted taxonomic practice in proposing the use of Sertellidae Jullien (1903) for the genera then grouped in the old family Reteporidae Smitt (1868), the type genus of which (*Retepora* Lamarck, 1801) appears to have no recognizable or acceptable type species. Levinsen (1902, 1909) had expanded the Reteporidae to include encrusting, non-fenestrate genera such as *Rhynchozoon* and *Schizotheca*.

Despite the objection of Harmer (1933), this arrangement is now generally accepted (e.g. Osburn 1952; Powell 1967).

The substantial number of genera of both erect and encrusting forms presently included in the Sertellidae appears to have several important morphological characteristics in common. The primary orifice, though widely variable in shape, typically has a denticulate or beaded distal rim ('vestibular arch'), and distinct condyles; the ovicell is imperforate, often prominent, and in most species is provided with a conspicuous frontal lip or labellum. In several genera (*Sertella*, *Schizotheca*, *Triphyllozoon*, for example) the ovicell is further characterized by a frontal fissure of variable size and extent. The peristome is often well developed, often with a notch, fissure or 'pseudospiramen' proximally, and frequently incorporating a suboral avicularium. Adventitious and vicarious avicularia occur in most genera.

The genera of erect species seem to constitute a fairly homogenous group, although some species diverge from the common pattern. *Schizoretepora tessellata* (Hincks), for example, has a smooth orifice rim and a minimal development of the peristome. The growth form of this species (see p. 108), and of the bilaminate species of *Reteporella* described by Hayward & Cook (1979), perhaps suggest a link with the encrusting genera *Schizotheca* and *Rhynchozoon*. The ovicell of the former, moreover, is very similar to those of *S. tessellata* and *Reteporella*. *Rhynchozoon* is characterized principally by its distinctly beaded orifice rim, by the ovicell, which has a frontal 'area' of uncalcified ectooecium and often possesses a short labellum, and by the peristomial complex, which includes a hammer- or anvil-shaped uncinate process projecting distally over the orifice. The uncinate process is variably developed; in the new species here assigned to *Rhynchozoon* it varies from an inconspicuous structure in *R. incallidum* to the massive development seen in *R. oscitans* and *R. stomachosum*. In *R. ptarmicum* there is no uncinate process; this fact caused some difficulty in deciding to which genus the species should be assigned, but in comparison with certain other species in the present collections prompted consideration of the systematic relationships of the Sertellidae with other family groups.

The genus *Brodiella* was introduced by Uttley & Bullivant (1972) for *Schizoporella longispinata* Busk. This well-defined species was first described (Busk 1884) from the Straits of Magellan, was reported from two localities in the Chatham Islands, New Zealand (Uttley & Bullivant 1972), and was found in the present collections. The affinities of *Brodiella* with *Rhynchozoon* seem clear; in both genera the zooid has a conspicuously beaded orifice and the ovicell typically develops a distinct labellum. On this basis Gautier (1962) referred the warm-temperate North Atlantic species, *Lepralia armata* Hincks, to *Rhynchozoon* and it is now clear (D. P. Gordon 1978, *in litt.*) that the species is correctly placed in *Brodiella*. Curiously, Uttley & Bullivant (1972) remarked upon the similarity of the two genera, yet assigned *Brodiella* to the Schizoporellidae. Although the *Meiring Naude* specimens of *B. ignota* sp. nov.

did not include ovicelled zooids, its morphology seems quite consistent with the generic diagnosis of *Brodiella*. The genus is here placed within the Sertellidae, emphasizing its relationship to *Rhynchozoon*. However, it must then be recognized that there is a need to consider the systematic affinities of two large and heterogenous genera, *Cleidochasma* Harmer and *Hippoporella* Canu, both currently assigned to the family Cleidochasmatidae Cheetham & Sandberg (1964). Species of both genera were present in the *Meiring Naude* collections.

Cleidochasma perspicua sp. nov. (p. 76) conforms most nearly to the diagnosis of *Cleidochasma*, although its ovicell, which has a well-marked frontal labellum, is clearly more similar to those of *Rhynchozoon* and *Brodiella* than the spherical, tuberculate ovicells of most species of *Cleidochasma*. A second species, *C. contractum* (Waters), figured by Cook (1964*b*: 15, fig. 5A), also has the same, typically Sertellid, ovicell morphology and, moreover, a finely denticulate orifice rim. *Hippoporella labiata* sp. nov. (p. 80) constitutes a more severe test of current systematics, and its inclusion in *Hippoporella* can only be regarded as a doubtful compromise. The morphology of the ovicell and the denticulate orifice rim again suggest an affinity with the encrusting genera placed among the Sertellidae, but the species does not conform strictly with the taxonomic diagnosis of any of them. The lepralioid orifice and prominent suboral umbo suggest that it might be temporarily accommodated in *Hippoporella*, particularly as this genus includes many tropical species (e.g. Harmer 1957: 1096. Cook 1964*b*: 8) that seem to have little in common with the boreal-arctic type species, *H. hippopus* (Smitt). The Australian species *Schizoporella pulchra* MacGillivray (1891: 81, pl. 9 (fig. 7)) illustrates the apparent convergence of characters in tropical, particularly Indo-West-Pacific, species of these different genera. *S. pulchra* forms encrusting, multilaminar colonies (e.g. BMNH 1897.5.1.758); the zooid has a broadly cleithridiate orifice with a finely denticulate distal rim. There are single or paired lateral oral avicularia, with short, distally directed, semicircular mandibles; one of these is frequently supplanted by an enlarged avicularium with a slender spatulate mandible. These avicularia seem to be interzooidal in origin and analogous to those seen in *Brodiella*, yet the tall basally jointed spines and proximal peristome rim characteristic of that genus are lacking in *S. pulchra*. The ovicell is prominent, frontally flattened, with a large area of uncalcified ectooecium and in the older parts of the colony the frontal walls of many zooids are obscured by massive, frontally budded, vicarious avicularia with broad scaphoid mandibles. These features are most usually associated with *Rhynchozoon*.

It seems clear, in conclusion, that any further investigation into systematic relationships within the Sertellidae must be combined with a thorough review of the morphology and systematics of many tropical species at present placed among the Cleidochasmatidae. The need for such a study is highlighted by the anomalous positions of several species reported upon here, but is beyond the scope of the present work.

Sertella Jullien, 1903

Sertella Jullien *in* Jullien & Calvet, 1903: 57. Hayward & Ryland, 1979: 260.

Sertella lata (Busk, 1884)

Fig. 24F–G

Retepora lata Busk, 1884: 115, pl. 27 (fig. 1).

Material

Stations SM 163, SM 179, SM 185.

Description

Colony generally thick and robust; trabeculae composed of three to seven longitudinal series of zooids, fenestrulae oval, small, 0,5–1,0 mm long. Primary orifice of zooid about twice as broad as long, lacking the usual denticulate rim; condyles basally deflected and not visible in frontal view. Peristome thin, with a central fissure and a small proximal pseudosinus, a single short spine present on each edge of peristome. Adventitious avicularia numerous, distributed over the entire frontal surface of the colony, mandible either semi-elliptical or acute triangular, mostly less than 0,1 mm long; rarely, an enlarged avicularium occurs, with a triangular mandible up to 0,15 mm long. Ovicell prominent, pear-shaped, convex, with a longitudinal frontal fissure and a very long labellum extending deep into the peristome. Basal surface of colony densely papillate, with a few scattered avicularia; frontal calcification becoming similarly papillate in later ontogenetic stages.

Remarks

The most characteristic feature of *Sertella lata* is the pear-shaped ovicell with its very long labellum. This feature was not illustrated by Busk (1884, pl. 27 (fig. 1)) who shows the ovicell orifice opening just above the level of the peristome. However, examination of the type specimen shows this detail to be incorrect, and in all respects it is in close correspondence with the *Meiring Naude* material. This species is known only from South Africa.

Sertella verecunda sp. nov.

Figs 25, 26A

Material

Holotype: SAM–A26446, station SM 185, 33°39,3′S 27°11,6′E, 90 m.

Description

Colony robust, holotype 6 mm high with a spread of 15 mm. Trabeculae stout, comprising five to eight longitudinal series of zooids, fenestrulae irregularly oval, up to 2 mm long. Zooids hexagonal or irregular, small, about 0,4 mm long by 0,2 mm broad; frontal calcification tessellated, with a few large

distinct marginal pores. Primary orifice transversely oval, deeply immersed and seen only at broken edges. Peristome tubular and deep, secondary orifice scarcely raised above frontal surface of zooid, a single pair of lateral oral spines present in early ontogeny; proximal border with a rounded notch, later closed forming a circular pseudosinus, persisting through later ontogenetic stages. Avicularia sporadically developed on frontal wall, one, two or more per zooid, either short, with a rounded rostrum bearing a semicircular mandible, a thick cross-bar and stout columella, or more elongate, almost bispatulate, with a semi-elliptical mandible, a centrally placed cross-bar and a delicate columella. The short type has a denticulate distal margin to the rostrum. Large vicarious avicularia distributed around edges of fenestrulae; rostrum quadrate, parallel-sided, palatal foramen triangular, cross-bar slender with a delicate columella. Ovicell pyriform, smooth surfaced, with an elongate central fissure and a short labellum; obscured by a thickened ooecial cover early in ontogeny. Basal surface of colony with both types of adventitious avicularia, often numerous.

Etymology

Verecundus (L.)—bashful, an allusion to the hidden primary orifice.

Remarks

S. verecunda may be distinguished from other species of *Sertella* by its pronounced pseudosinus, and the absence of peristomial avicularia, by the two types of adventitious avicularia, and by the characteristic quadrate fenestral avicularia.

Schizoretepora Gregory, 1893

Schizoretepora Gregory, 1893: 224. Harmer, 1933: 619.

Schizoretepora tessellata (Hincks, 1878)

Fig. 24H

Retepora tessellata Hincks, 1878: 358, pl. 19 (figs 9–12). Busk, 1884: 112, pl. 27 (fig. 8). O'Donoghue & De Watteville, 1935: 210; 1937: 15. O'Donoghue, 1957: 91.

Material

Stations SM 163, SM 163/164, SM 180, SM 185.

Description

Colony rather delicate; trabeculae composed of four to six longitudinal series of zooids, or up to eight at points of trabecular fusion, fenestrulae elongate-oval, up to 1,6 mm long. Zooids hexagonal or irregular, rather flat, separated by distinct sutures at first, boundaries later indistinct. Primary orifice semi-elliptical, longer than wide; distal border smooth, proximal border gently concave, with a short notch-like sinus. Peristome developing initially as a thin erect flange on each side of the orifice, not developed proximally; later

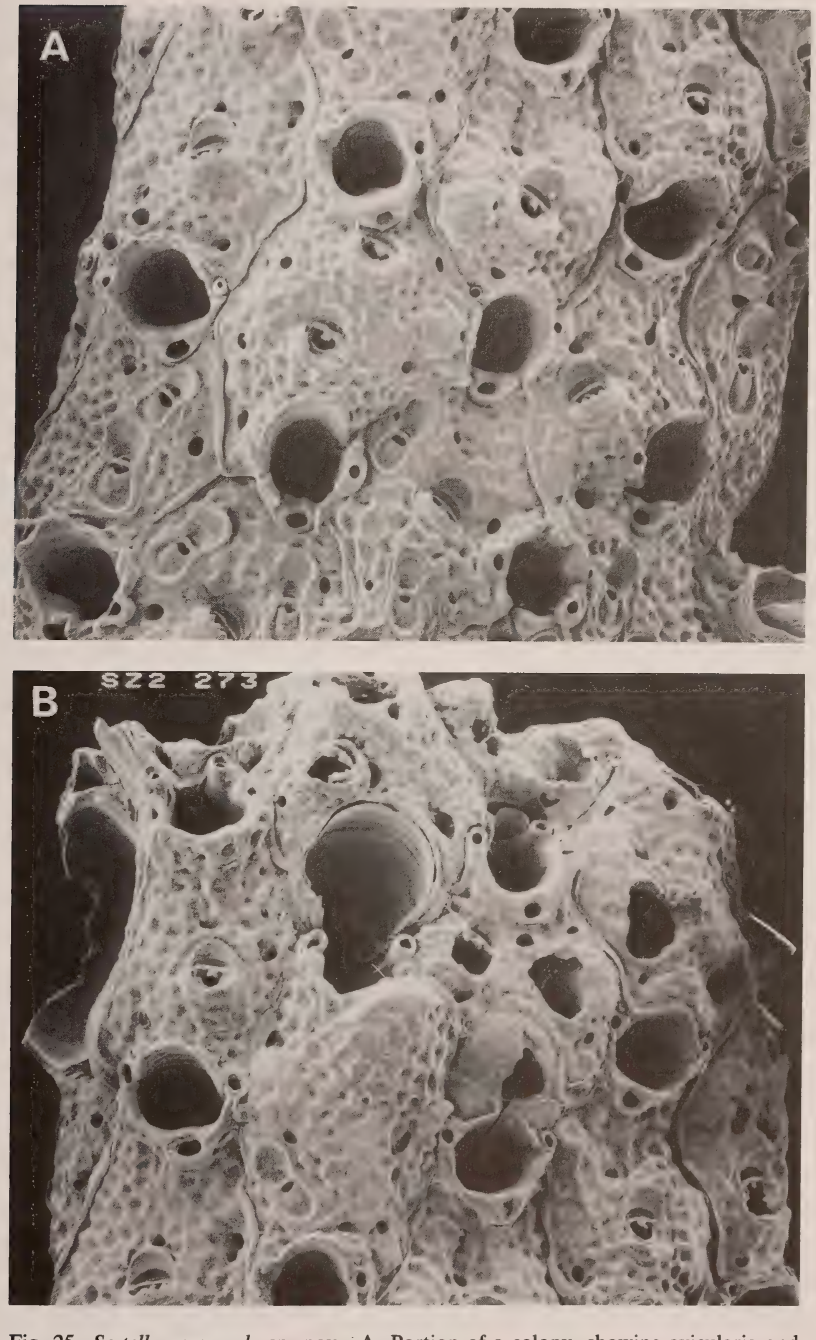

Fig. 25. *Sertella verecunda* sp. nov. A. Portion of a colony, showing avicularia and pseudospiramina. × 100. B. Zooids from the growing tip of a branch, with developing ovicells. × 100.

immersed and somewhat unclear, but proximal side of orifice still distinct. Up to six distal and lateral oral spines present, only the proximal pair of which persist as secondary calcification proceeds. Frontal calcification finely granular with a small number of marginal pores. Avicularia variably developed; frequently proximolateral to orifice, small, with a semi-elliptical mandible; also elsewhere on frontal wall, small, with more elongate, semi-elliptical or acute triangular mandibles. Gigantic avicularia typically frequent; cystid obscuring most of the zooid bearing it, rostrum elongate, acute triangular, up to 0,3 mm long, perpendicular to frontal plane of zooid. Ovicell prominent, spherical, with a conspicuous oval orifice situated well above peristome rim. Basal surface sutured, with numerous small avicularia and typically a gigantic avicularium at the proximal end of each fenestrula.

Remarks

Schizoretepora tessellata is unusual among the Sertellidae in possessing the facility to grow as a typical fenestrate colony, or as a folded bilaminar sheet. This facility may be expressed in a single colony, with substantial bilaminate colonies producing peripheral fenestrulae (e.g. BMNH 1962.6.4.17pt., Millers Point, Cape Town). Described originally from South Australia, it was reported from Simon's Bay (Cape of Good Hope) by Busk (1884). Comparison of Australian and South African specimens with the *Meiring Naude* samples shows some variation in the width of the primary orifice both between and within each of the three series of specimens. Additionally, some of the Australian specimens develop long (0,8 mm) antenniform spines. However, the avicularia and ovicells are closely comparable in all instances.

Reteporella Busk, 1884

Reteporella Busk, 1884: 126. Harmer, 1934: 572.

Reteporella dinotorhynchus Hayward & Cook, 1979

Fig. 24E

Reteporella dinotorhynchus Hayward & Cook, 1979: 95, fig. 14A–D.

Material

Stations SM 163, SM 163/164, SM 184, SM 185.

Remarks

The material from station SM 185 comprised a more complete ontogenetic sequence than was provided by the first *Meiring Naude* samples, and it is clear that the original description of this species must be amplified. In particular, it is evident that a small adventitious avicularium develops on the peristome adjacent to the lateral notch. This is missing in even the least worn fragments, and is obscured by the peristome in the oldest parts of the colony. Developing

ovicells were found in the present specimens, but no complete examples remained; the ovicell seems to have a substantial frontal fissure.

Iodictyum Harmer, 1933

Iodictyum Harmer, 1933: 624; 1934: 537.

Iodictyum flosculum sp. nov.

Fig. 27A–C

Material

Holotype: SAM–A26447, station SM 164, 33°04,6′S 28°06,6′E, 90 m.
Other material: stations SM 163, SM 185.

Description

Colony white, forming a delicate cup shape, up to 8 mm high with a spread of 6 mm in present material; trabeculae composed of three alternating series of zooids, increasing to four or five at trabecular fusion, fenestrulae elongate-oval, up to 0,8 mm long. Zooids quadrate, rather flat, separated by distinct raised sutures; calcification smooth, imperforate except for a few rather large round marginal pores, usually situated at the proximal end of the zooid. Primary orifice semicircular, distal edge not denticulate, proximal edge slightly concave, with large blunt lateral condyles. Peristome characteristic of genus: developed early in ontogeny and completely hiding orifice; erect, broadly flared, the free edge drawn into a number of delicate spikes, aligned with a second series of smaller spikes around the inner rim of the peristome. The inner denticulations of the peristome are continuous with delicate ridges which extend down its interior surfaces; proximally, two of the ridges delimit a U-shaped channel which appears as a distinct pseudosinus in damaged zooids. With increasing calcification the peristome is immersed, the outer spikes are lost and the aperture appears as a simple denticulate opening. Avicularia infrequent, orientated oblique to proximal edge of peristome, rostrum elongate, subtriangular, hooked at tip. Ovicell not found. Basal surface of colony faintly papillate, crossed by conspicuous sutures, lacking avicularia.

Etymology

Flosculus (L.)—a little flower.

Remarks

This delicate species represents the first occurrence of the genus *Iodictyum* remote from the western Pacific.

Measurements (means of 20 values) in mm

Lz	lz
0,42	0,19

Rhynchozoon Hincks, 1895

Rhynchozoon Hincks, 1895: V. Hayward & Ryland, 1979: 271.

This large and difficult genus is widely distributed in both temperate and tropical waters. Most bryozoan faunas of the continental shelf seas include one or more species of *Rhynchozoon*, yet few of these are adequately characterized and taxonomic confusion obscures the identity of most of them. In almost all species of *Rhynchozoon* the primary orifice of the zooid becomes immersed in a secondarily developed peristomial complex which is frequently ornamented with a variety of knobs and processes, and there is often a proliferation of small adventitious avicularia. These later stages of ontogeny are often subject to great variation within a single colony and cannot be used as reliable specific characters. The shape of the primary orifice and the morphology of the suboral avicularium, together with its uncinate process, should be used as the most important features for discriminating between species and it is clear that when this is done a greater diversity of species is revealed than is apparent from the literature (e.g. Hayward 1974). These features, together with selected secondary characters, show that the South African fauna includes a rich variety of species, none of which from among those represented here may be identified with either of the two species described by O'Donoghue & De Watteville (1935), or with any of the Indo-West-Pacific species reported by Harmer (1957).

Rhynchozoon documentum sp. nov.

Fig. 26B–C

Material

Holotype: SAM–A26448, station SM 163/164, 33°04,6′S 28°06,6′E, 90 m.
Other material: stations SM 163, SM 164.

Description

Colony encrusting, multilaminar, forming small nodular sheets. Zooids distinct only at growing edge, oval and convex; frontal wall smooth, with large marginal pores. Primary orifice broader than long; anter transversely oval, with finely denticulate rim, poster forming a short, U-shaped sinus, oral spines lacking. Suboral avicularium large, distinct in early ontogenetic stages, mandible elongate elliptical, uncinate process well developed and conspicuous, delimiting laterally a closed pseudosinus. Peristome developing a thickened rim obscuring primary orifice and suboral avicularium; proximally a median fissure is flanked by short conical processes, in later ontogeny further short columnar processes are developed around the whole of the secondary orifice. Frontal avicularia often numerous, small, with semicircular or semi-elliptical mandibles.

Etymology

Documentum (L.)—an example.

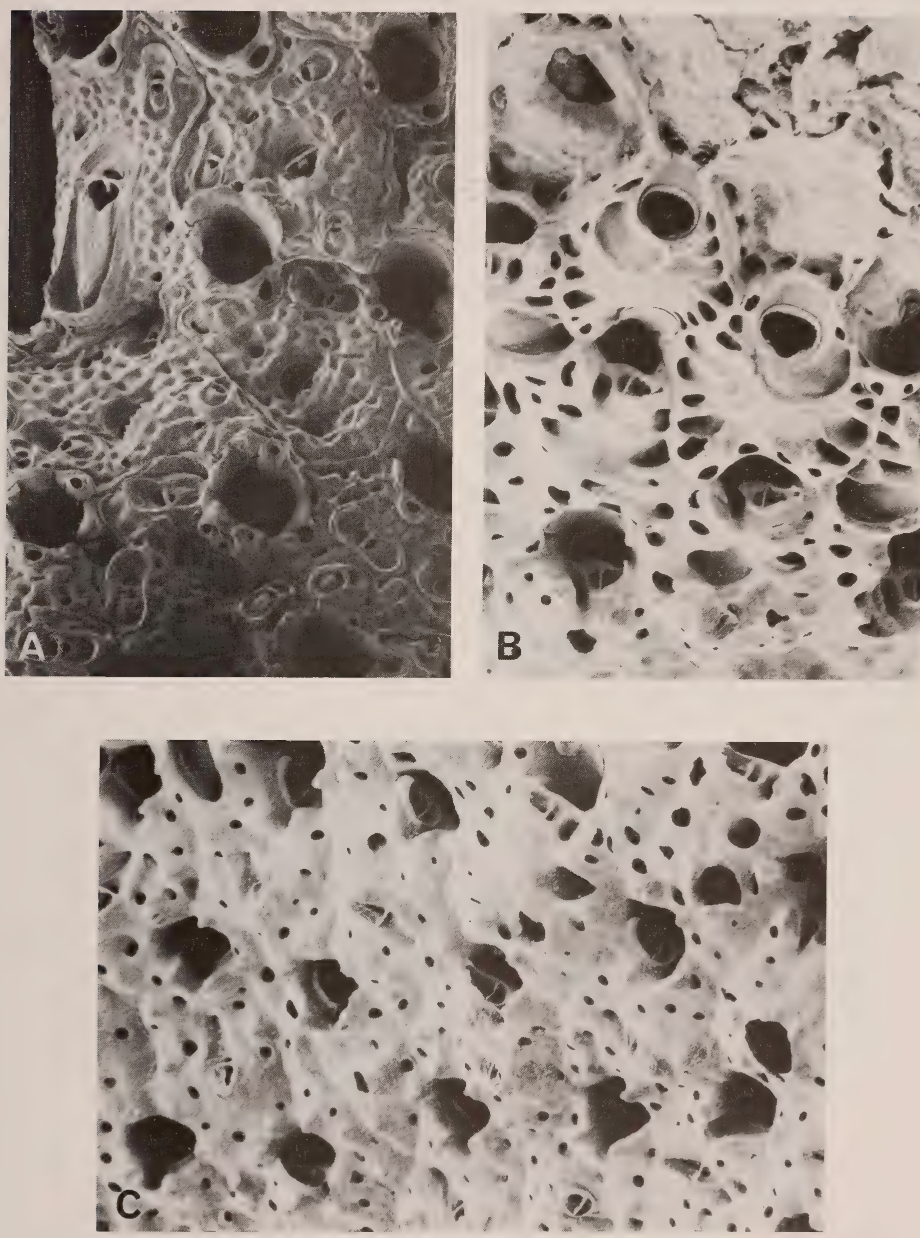

Fig. 26. A. *Sertella verecunda* sp. nov., the edge of a fenestrula (left) with a vicarious avicularium. × 96. B–C. *Rhynchozoon documentum* sp. nov. B. Zooids at a growing edge, note primary orifice and conspicuous areolae. × 76. C. Later zooids, each with one frontal avicularium and conspicuous areolae. × 64,3.

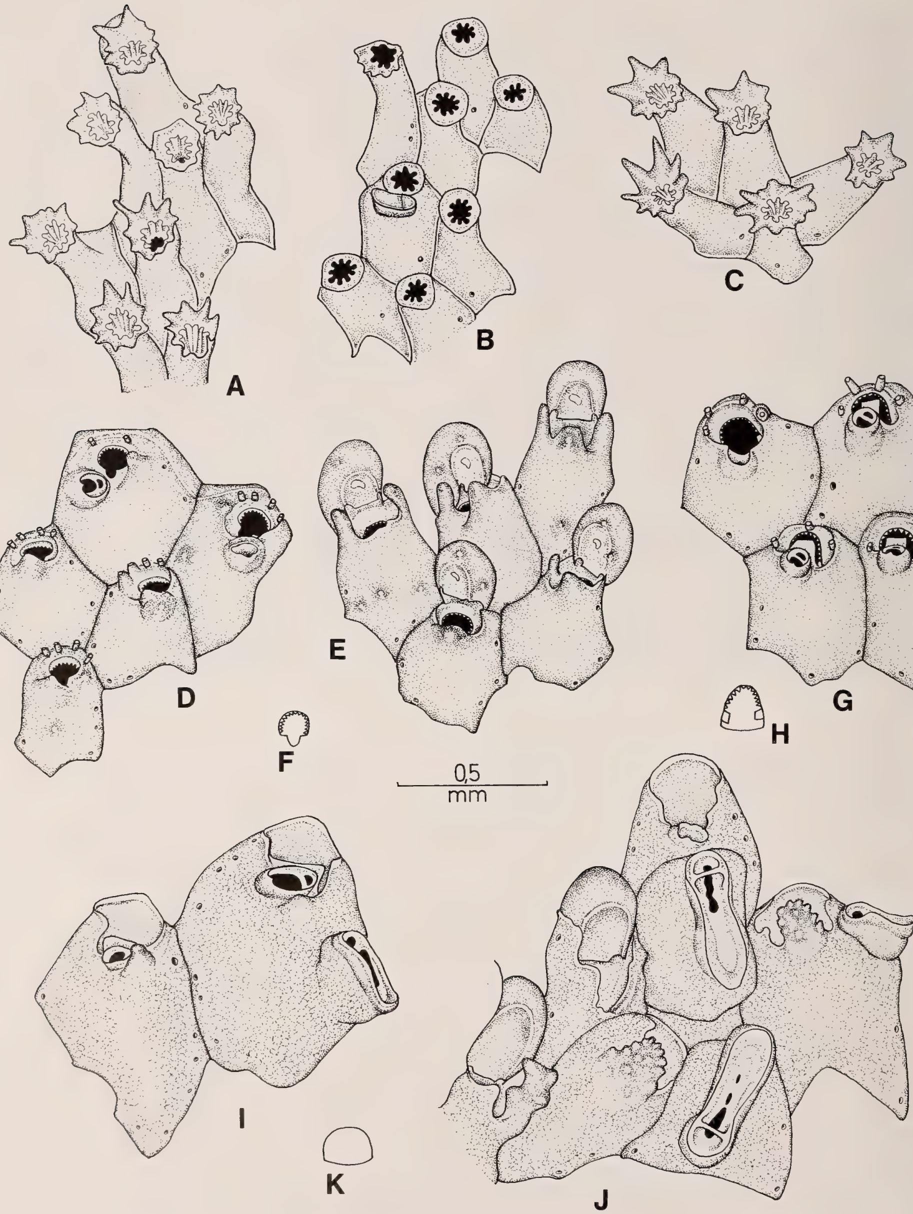

Fig. 27. A–C. *Iodictyum flosculum* sp. nov. A. Young zooids showing typical flared spinose peristomes. B. Old zooids with worn peristomes; a single suboral avicularium. C. a complete juvenile colony, possibly including the ancestrula. D–F. *Rhynchozoon incallidum* sp. nov. D. Zooids from the growing edge. E. Later zooids, with ovicells and developed peristomes. F. Outline diagram of primary orifice. G–H. *Rhynchozoon oscitans* sp. nov. G. Four young zooids; note conspicuous uncinate process. H. Outline diagram of primary orifice. I–K. *Rhynchozoon stomachosum* sp. nov. I. Two young zooids. J. Later zooids, with typical development of the umbo, and two vicarious avicularia. K. Outline diagram of the primary orifice.

Remarks

In later ontogenetic stages the marginal pores of the zooids are particularly distinct, appearing as elongate tubular structures within the rather vitreous calcification, and appear to be associated with the production of numerous small adventitious avicularia. This particularly conspicuous morphological feature seems to be a fairly constant characteristic of this species.

Measurements (means of 20 values) in mm

Lz	lz
0,39	0,32

Rhynchozoon beatulum sp. nov.

Fig. 28

Material

Holotype: SAM–A26449, station SM 163, 33°04,6′S 28°06,6′E, 90 m.
Other material: stations SM 163/164, SM 184, SM 185.

Description

Colony encrusting, forming small irregular sheets, apparently unilaminar. Zooids oval to hexagonal, strongly convex; frontal wall finely granular, becoming increasingly vitreous in later ontogenetic stages, marginal pores conspicuous. Primary orifice wider than long; anter orbicular, with finely denticulate rim, poster broad, shallowly concave, two short, widely-spaced, distal oral spines present in newly budded zooids. Suboral avicularium large and distinct, rostrum hooked, with elongate triangular mandible; uncinate process bluntly triangular. Peristomial thickening moderate: a short, blunt umbo develops on the cystid of the avicularium, and a second umbo on the opposite lateral edge of the secondary aperture, with a small asymmetrically developed notch between; in later ontogenetic stages, one or two short knobs may be developed on the distal rim of the peristome. Frontal avicularia typically limited to one on each zooid, on the proximal half of the frontal wall; rostrum triangular, directed proximally. Ovicell rather elongate, with an oval area of uncovered entooecium frontally, and a large frontal labellum; obscured by a thickened ooecial cover.

Etymology

Beatus (L.)—happy, an allusion to the broad sinus.

Remarks

Despite the progressive thickening of the frontal calcification in later ontogeny, the marginal pores of *R. beatulum* remain distinct. Further, the suboral avicularium is rarely completely hidden, and the peristomial rim shows

only a limited development of umbones. The frontal avicularium is remarkably constant in position, shape and orientation in all the present specimens, and assists in distinguishing this species from others in the South African fauna.

Measurements (means of 20 values) in mm

Lz	lz
0,45	0,35

Rhynchozoon incallidum sp. nov.

Figs 27D–F, 29A–B

Material

Holotype: SAM–A26450, station SM 185, 33°39,3′S 27°11,6′E, 90 m.
Other material: stations SM 163, SM 163/164, SM 180, SM 184.

Description

Colony encrusting, forming small unilaminar patches. Zooids oval to hexagonal, frontal wall smooth and vitreous with few indistinct marginal pores. Primary orifice as wide as long: anter semicircular, with finely denticulate rim, poster forming a short quadrate sinus; up to four slender distal oral spines present. Suboral avicularium on a voluminous cystid, developed apically as a blunt umbo; rostrum triangular, perpendicular to frontal plane of zooid and facing laterally, uncinate process poorly developed, not prominent. A second umbo typically developed on opposite lateral border of orifice, a third may be present distal to the suboral avicularium; these develop independently of the spine bases. Frontal avicularia not found. Ovicell spherical, flattened frontally, with an irregular area of uncovered entooecium and a short, broad labellum. Ooecial cover developing early in ontogeny, frequently with one or more low umbones, but ovicell remaining conspicuous. Zooid boundaries become indistinct in later ontogenetic stages, additional umbones may be developed on the frontal wall, but the primary orifice is not deeply immersed and generally remains visible in frontal view.

Etymology

Incallidus (L.)—simple, referring to the relative simplicity of the zooidal morphology.

Remarks

The shape of the primary orifice, the poor development of the uncinate process and the relatively simple zooid morphology serve to distinguish *R. incallidum* from other species of *Rhynchozoon*.

Measurements (means of 20 values) in mm

Lz	lz
0,45	0,32

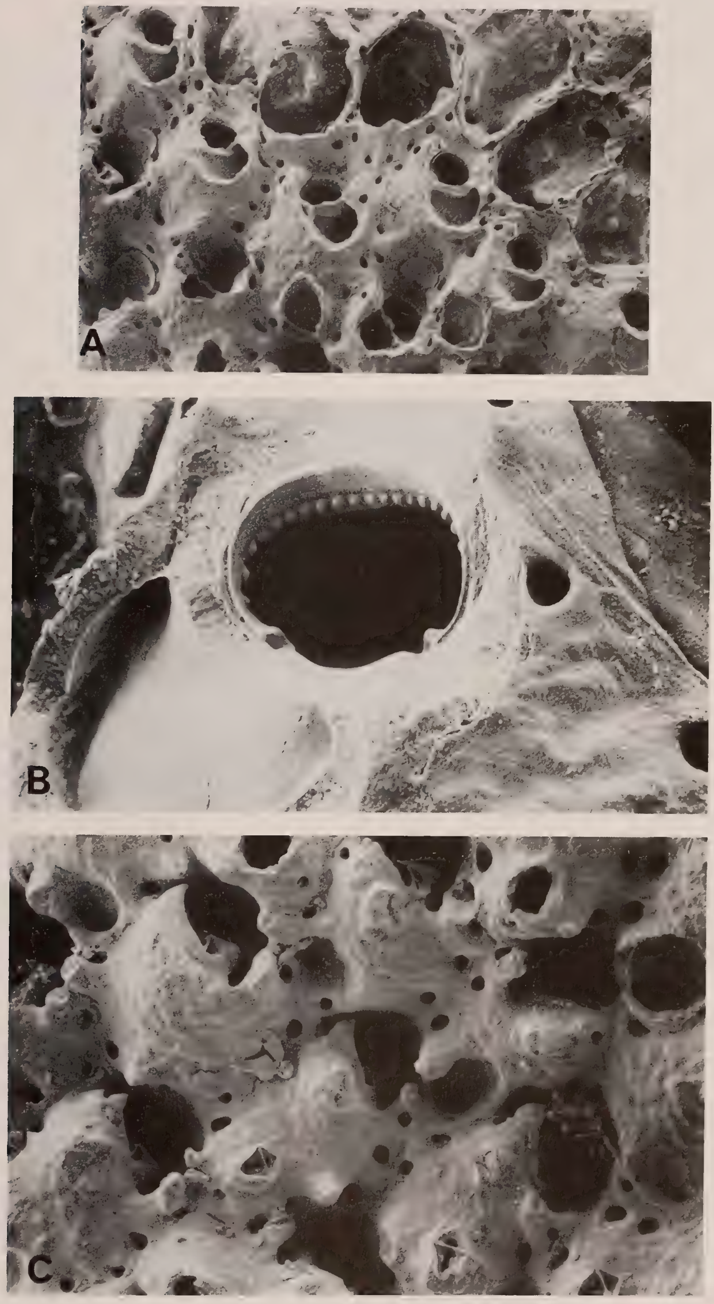

Fig. 28. *Rhynchozoon beatulum* sp. nov. A. Zooids at a growing edge. × 46,5. B. Details of a primary orifice. × 240. C. Later zooids, showing the characteristic frontal avicularium. × 61.

Rhynchozoon oscitans sp. nov.

Fig. 27G–H

Material

Holotype: SAM–A26451, station SM 185, 33°39,3′S 27°11,6′E, 90 m.
Other material: station SM 180.

Description

Colony encrusting, unilaminar. Zooids oval to hexagonal, convex, distinct, separated by well-marked sutures. Frontal calcification thick and smooth, with a few inconspicuous marginal pores. Primary orifice longer than wide, lepralioid; proximal edge straight, distolateral rim denticulate above massive rectangular, basally deflected condyles. Four or five oral spines present, the distalmost pair persisting as short stumps in later ontogeny. Peristome low; suboral avicularium situated medioproximally on outer peristome rim, at oblique angle to frontal plane, mandible small, semi-elliptical. Uncinate process large, quadrate, very conspicuous. Frontal avicularia and ovicells not found.

Etymology

Oscitans (L.)—yawning, referring to the conspicuous primary orifice.

Remarks

Only two small specimens of this species were found, and neither represents a complete astogenetic or ontogenetic sequence. However, the shape of the orifice, and the massive uncinate process are very distinctive and sufficient to distinguish *R. oscitans* from all known species of *Rhynchozoon*.

Measurements (means of 20 values) in mm

Lz	lz
0,53	0,37

Rhynchozoon stomachosum sp. nov.

Fig. 27I–K, 29C

Material

Holotype: SAM–A26452, station SM 234, 32°15′S 29°09,1′E, 500–520 m.

Description

Colony encrusting, multilaminar. Zooids at growing edge large, oval and convex; frontal calcification granular, becoming rather nodular in later ontogenetic stages, marginal pores few and small but distinct. Primary orifice D-shaped, wider than long; proximal border almost straight, distolateral rim

Fig. 29. A–B. *Rhynchozoon incallidum* sp. nov. A. A group of zooids from a dead colony. × 100. B. Detail to show primary orifice and spine bases. × 300. C. *Rhynchozoon stomachosum* sp. nov. × 41.

finely denticulate, apparently without condyles. No oral spines. Suboral avicularium obliquely transverse to orifice, at a slight angle to frontal plane; rostrum triangular, with hooked tip. Uncinate process large and conspicuous. Peristome morphology variable; typically developing a columnar, clavate umbo proximomedially, with a knobbed granular surface, adjacent to a shallow notch; two, rarely more, short processes may also be present on the lateral borders of the peristome. Alternatively, two shorter, more slender, equisized umbones may develop, flanking a more prominent peristomial notch. Frontal avicularia of two sizes: on peripheral zooids situated laterally, close to suture, and directed proximolaterally, the plane of the palate typically at a right angle to the frontal plane; in later ontogeny a larger avicularium may develop on the frontal wall along the midline of the zooid, directed proximally with the plane of the palate normal to the frontal plane. In both types the rostrum is elongate, slightly expanded distally to give a slender spatulate shape, straight or gently curved laterally; cross-bar entire, palate with a narrow, elongate central fissure. Ovicell longer than wide, flattened frontally, with a distinct labellum; frontal ectooecium finely tuberculate.

Etymology

Stomachosus (L.)—irritable, an allusion to the aggressive aspect of the peristomial complex.

Remarks

The material comprised a single colony, 20 mm in diameter, with an undulating, unilaminar growing edge and a thickened multilaminar central region. The calcification is thick, particularly that of the basal walls; the basal surface of the colony was apparently mostly unattached to the substratum, and is encrusted with epizooites.

Measurements (means of 20 values) in mm

Lz	lz
0,77	0,54

Rhynchozoon ptarmicum sp. nov.

Fig. 30

Material

Holotype: SAM–A26453, station SM 179, 33°30,3′S 27°22,1′E, 80 m.
Other material: stations SM 185, SM 239, SM 250.

Description

Colony encrusting, multilaminar, forming extensive nodular sheets. Zooids convex, large; frontal calcification thick and vitreous, becoming

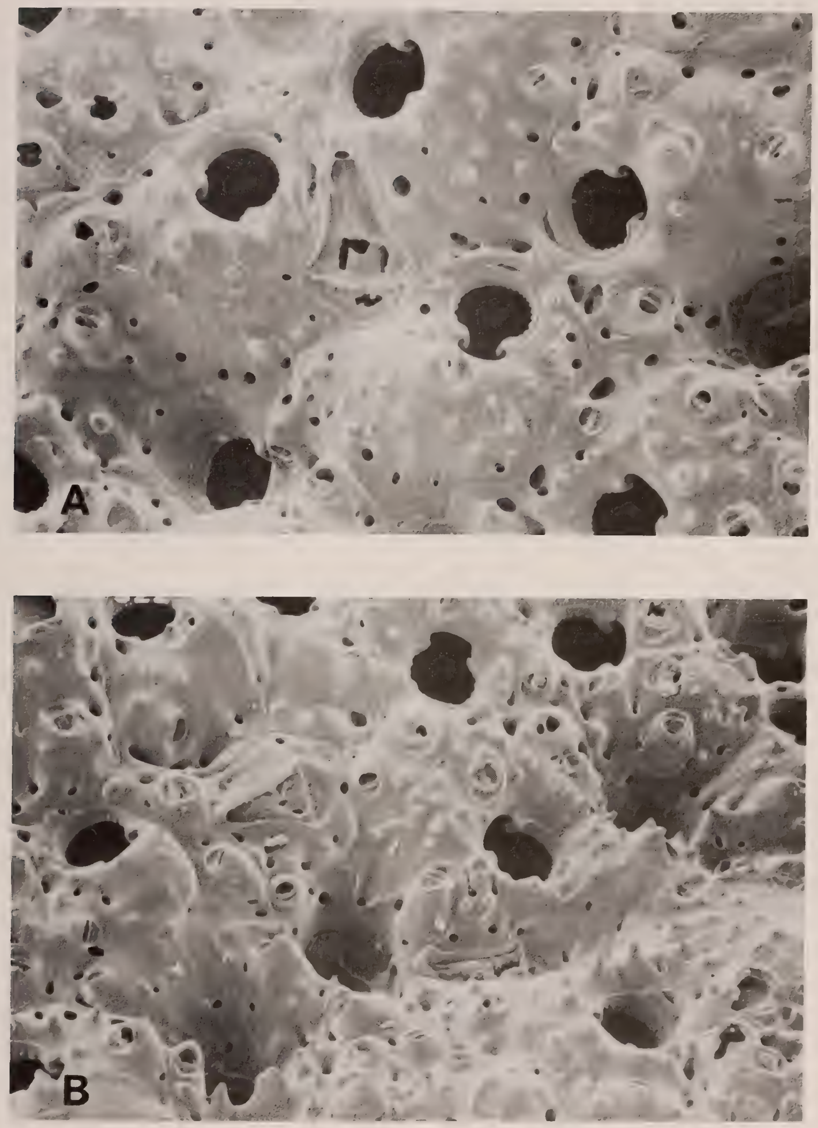

Fig. 30. *Rhynchozoon ptarmicum* sp. nov. A. Young zooids, showing the form of the primary orifice. × 67. B. Later zooids, showing proliferation of avicularia and orifices immersed in thickened calcification. × 50.

distinctly nodular in later ontogeny, marginal pores small. Primary orifice slightly longer than wide; anter orbicular, with finely denticulate rim, poster shallow, transversely elliptical; condyles large and conspicuous, triangular, basally deflected. Four to six distal oral spines present in early ontogeny, obscured by the development of a low thickened peristome, bearing a number of short conical umbones. Suboral avicularium small, not enveloped by the peristome and always distinct, rostrum at acute angle to frontal plane, directed obliquely laterally, mandible short, broadly subtriangular; sporadically developed and frequently absent. No uncinate process. Additional avicularia often abundant, of two types: small, adventitious, with a rounded cystid and short semicircular or subtriangular mandible, developed along lateral borders of zooid and encroaching on to frontal wall, often numerous, up to ten per zooid; large, ?vicarious, with a swollen cystid supporting an elongate, triangular, hooked rostrum (0,35 mm), with complete cross-bar and massive, quadrate, bifid columnella. A slightly smaller version of the latter type (?adventitious) may replace the suboral avicularium in some zooids. Ovicell elongate oval, frontal surface granular, striated, labellum distinct; ooecial cover developed in later ontogeny, often tuberculate.

Etymology

Ptarmos (Gr.)—a sneeze, an allusion to the open aspect of the orifice.

Remarks

Live colonies were collected from all four stations, the largest (SM 179) was a massive, nodular, multilaminar growth measuring 70 mm by 35 mm. The young colonies from SM 185 had a pale blue-grey coloration. The ?vicarious avicularia resemble those of *Strophiella tuberigera* Jullien & Calvet (1903: 66, pl. 9 (fig. 1)), reported from the Gulf of Gascony, from 135 m. *S. tuberigera* has a 'beaded' orifice and is probably referable to *Rhynchozoon*; it differs completely from *R. ptarmicum* in the shape of the primary orifice.

Measurements (means of 20 values) in mm

Lz	lz
0,73	0,52

Brodiella Uttley & Bullivant, 1972

Brodiella Uttley & Bullivant, 1972: 35.

Brodiella longispinata (Busk, 1884)

Fig. 31A–B

Schizoporella longispinata Busk, 1884: 163, pl. 17 (figs 2A, C).
Brodiella longispinata: Uttley & Bullivant, 1972: 36, fig. 26.

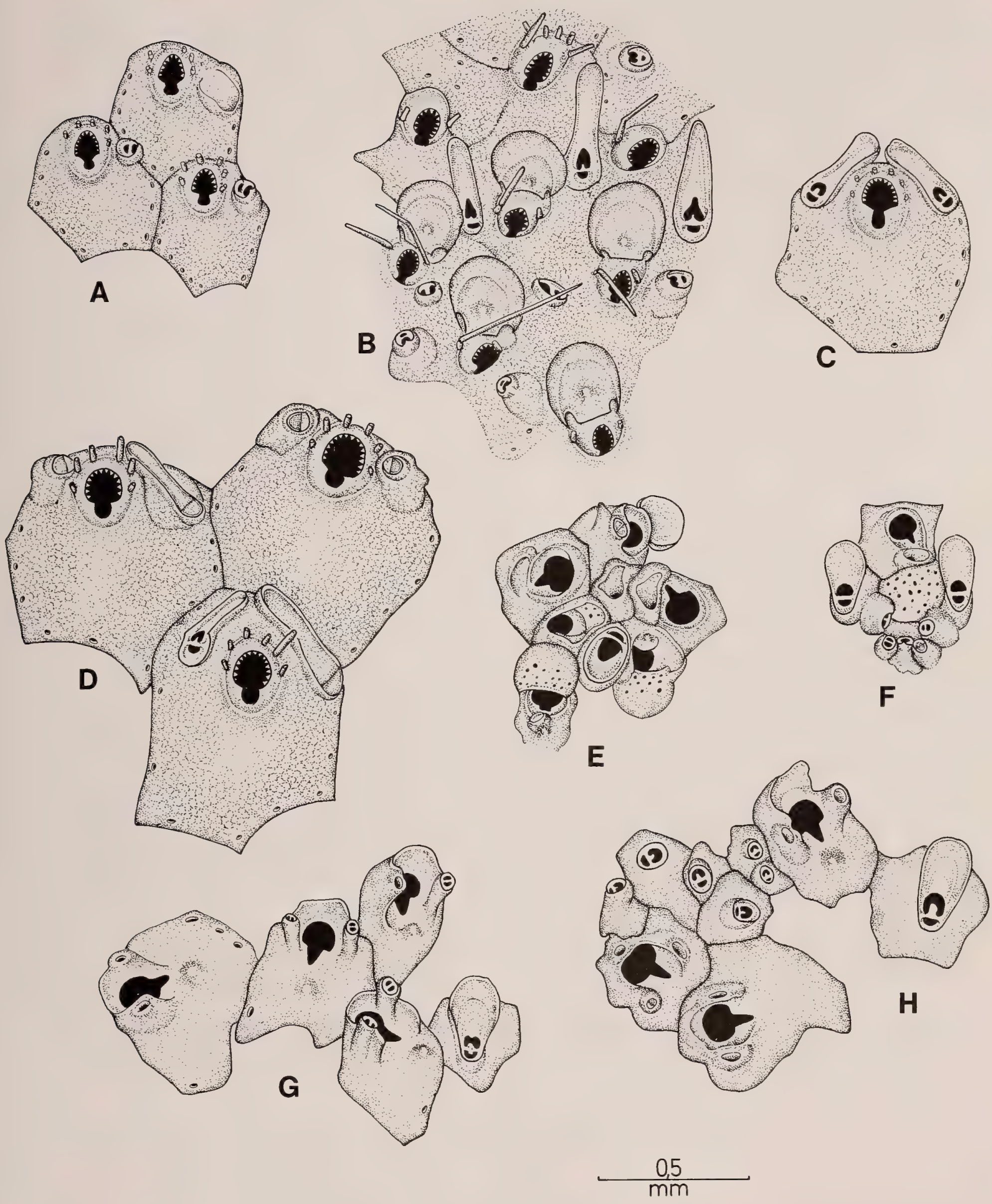

Fig. 31. A–B. *Brodiella longispinata* (Busk). A. Three young zooids. B. Portion of a colony showing ovicells and different types of avicularia. C–D. *Brodiella ignota* sp. nov. C. A typical zooid. D. Three zooids showing variation in avicularia type. E–F. *Turbicellepora conica* (Busk). E. Portion of a colony showing active frontal budding. F. Vicarious avicularia, and adventitious avicularia clustered on the peristome rim of a brooding zooid. G–H. *Turbicellepora valligera* sp. nov. G. Young zooids, showing typical development of the peristome. H. Zooids from an older part of the colony, with numerous small avicularia.

Material

Stations SM 185, SM 239.

Description

Colony encrusting, multilaminar. Zooids oval to hexagonal, heavily calcified, separated by distinct grooves at first, boundaries later obscured by secondary calcification. Primary orifice cleithridiate: anter orbicular, with a denticulate rim, separated from the short rounded poster by prominent condyles; operculum well chitinized, dark brown, with a distinct marginal sclerite and a longitudinal median groove. Six distal oral spines, jointed basally, of variable length, often greatly enlarged. Proximal side of orifice enclosed by a low, thickened, peristomial rim, extending between the bases of the most proximal pair of spines. Frontal wall thick, vitreous, with a characteristic surface of rounded nodules imparting a rippled effect; marginal pores infrequent and not readily visible. Avicularia adventitious, lateral to orifice, single or paired, cystid low, tumid, rostrum elliptical, pivotal bar stout with a thickened columnella, mandible semi-elliptical, directed laterally or obliquely distally. Either or both avicularia may be replaced by an enlarged type with an elongate, acute triangular mandible directed distally; alternatively or additionally this enlarged avicularium may occur on the frontal wall, when the mandible is directed proximally. Ovicell prominent, almost perpendicular to frontal plane of zooid, oval, flattened frontally, with a short quadrate labellum above the aperture and an uncovered frontal area of entooecium.

Remarks

The incidence of the different types of avicularia varies, and the larger type may be more common than the small in some specimens. Both types are seen in Busk's original specimen (BMNH 1887.12.9.653), which in other respects as well differs in no way from the *Meiring Naude* material.

Distribution

Brodiella longispinata was described by Busk (1884) from the Straits of Magellan and has been reported subsequently from New Zealand and the Chatham Islands (Uttley & Bullivant 1972). A synonymy of recent and fossil New Zealand records is given by these authors.

Brodiella ignota sp. nov.

Fig. 31C–D

Material

Holotype: SAM–A26454, station SM 250, 31°59,3′S 29°22,5′E, 150–200 m.

Description

Colony encrusting, multilaminar. Zooids oval to hexagonal, large and broad, convex, separated by distinct grooves. Primary orifice comprising an

orbicular anter, with finely denticulate rim, and a short, rounded poster below blunt condyles. Six or seven slender, distal oral spines; proximally, a thin peristomial rim encloses the orifice between the proximalmost pair of spines, particularly developed in heavily calcified older zooids. Frontal wall thick, vitreous and glistening, surface texture of densely packed rounded nodules; marginal pores few in number, small and inconspicuous, generally visible only in newly budded zooids. Avicularia paired, situated lateral to distal half of orifice; cystid small, tumid, rostrum elliptical, directed laterally or medially, mandible semicircular. Either or both avicularia frequently replaced by an enlarged type with an elongate spatulate mandible directed distomedially, close to distal border of orifice, reminiscent of *Hippaliosina*; palate with a small foramen almost occluded by a thick columella. Rarely, one or both types of avicularia may occur on the frontal wall. Small basal pore chambers present. Ovicells not found.

Etymology

Ignotus (L.)—unknown.

Remarks

The dimorphic avicularia, arising close to the primary orifice, the denticulate anter, the peristomial rim and the characteristically thick, nodular and vitreous frontal wall are all features of *Brodiella*, exemplified in the type species *B. longispinata* (above). *B. ignota* differs from that species in the proportions of the orifice, the shape and orientation of the enlarged avicularia and in possessing more slender oral spines. D. P. Gordon (1979 *in litt.*) has pointed out that the northern hemisphere species *Lepralia armata* Hincks (Hayward & Ryland 1979: 206, as *Buffonellaria*) also belongs to *Brodiella*.

Measurements (means of 20 values) in mm

Lz	lz
0,83	0,61

Family **Celleporidae** Busk, 1852

Celleporidae Busk, 1852: 85. Hayward & Ryland, 1979: 274.

Turbicellepora Ryland, 1963

Turbicellepora Ryland, 1963: 34. Hayward & Ryland, 1979: 284.

Turbicellepora conica (Busk, 1884)

Fig. 31E–F

Cellepora conica Busk, 1884: 203, pl. 28 (fig. 10), pl. 36 (fig. 1).

Material

Stations SM 163, SM 163/164, SM 164, SM 179, SM 180, SM 184, SM 185.

Description

Colony forming small nodules on erect substrata, pisiform, or branching in one or more planes to give a stellate appearance. Zooids closely packed, individual boundaries scarcely discernible. Primary orifice longer than broad; anter suborbicular, poster deep, V-shaped, constituting one-third of total orifice length. Peristome thin, tubular, incorporating proximolaterally a short cylindrical avicularium; mandible semi-elliptical or subtriangular, acute to frontal plane, directed obliquely laterally. Ovicell prominent, thinly calcified, frontal surface closely punctured by numerous small round pores. Vicarious avicularia of two types: elongate, broadly elliptical or slightly spatulate, with thin cross-bar and large palatal foramen, small (0,2 mm long) and generally infrequent; outnumbered by small vicarious avicularia, identical to suboral type, with semi-elliptical mandible.

Remarks

The peristome tends to encircle the orifice completely, extending on to the lateral regions of the ovicell. On older zooids the small avicularia tend to multiply and typically become clustered around the rim of the deeply immersed peristome, four or five commonly occur together. However, this very characteristic feature seems to be present only in colonies in which growth by frontal budding has slowed, in young colonies the continued budding of zooids results in a surface composed of numerous cylindrical peristomes. The multiplication of these small avicularia is thus apparently an ontogenetic, and possibly gerontic, effect.

Turbicellepora conica is known only from Simon's Bay, South Africa (BMNH 1899.7.1.482, 483, 484, 486).

Measurements (means of 20 values) in mm

Lor	lor
0,14	0,11

Turbicellepora valligera sp. nov.

Fig. 31G–H

Material

Holotype: SAM–A26455, station SM 163, 33°04,6′S 28°06,6′E, 90 m.
Other material: station SM 239.

Description

Colony developing from an encrusting base, forming a slender, erect cylindrical growth. Zooids distinct, strongly convex and thickly calcified; frontal wall fine-grained and smooth, with three or four very large marginal pores. Primary orifice longer than broad, with a deep V-shaped poster comprising

about one-third of the total length; hooded distally by a thin, erect peristomial rim, the free edge of which is often peaked medially or produced into two or more processes. Paired lateral oral avicularia; slender, cylindrical, with small semicircular mandibles, linked distally by the peristome. Proximal to orifice a conspicuous median umbo develops, often produced into an erect spike. Vicarious avicularia of two types: broadly spatulate, cross-bar slender with a thick median columella, palate with a small foramen; small, oval, with a semicircular mandible, often abundant.

Etymology

Vallum (L.)—a palisade, referring to the enveloping peristome.

Remarks

This species is superficially similar to *Osthimosia bicornis* (Busk) from which it differs in the position of the oral avicularia, which are proximolateral in *O. bicornis*. Further, the ovicell of *O. bicornis* has the single central pore characteristic of the genus; only a single partly immersed ovicell was found on the material of *T. valligera*, but it was typical of *Turbicellepora*, being closely punctured by small pores. The numerous small vicarious avicularia are also seen in *T. pustulata* (Busk), but this species is characterized by a single lateral oral avicularium, and the absence of the columella on the cross-bar of the spatulate avicularium.

Measurements (means of 20 values) in mm

Lor	lor
0,15	0,12

Celleporaria Lamouroux, 1821

Celleporaria Lamouroux, 1821: 43. Harmer, 1957: 663.

Celleporaria tridenticulata (Busk, 1881)

Fig. 19H

Cellepora tridenticulata Busk, 1881: 343, pl. 26 (fig. 9).
Celleporaria tridenticulata: Harmer, 1957: 670, pl. 42 (figs 5–10).

Material

Stations SM 162, SM 163, SM 163/164, SM 164.

Description

Colony encrusting, multilaminar, forming small nodules. Zooids oval, convex, separated by distinct grooves; boundaries distinct in peripheral zooids, later obscured. Primary orifice D-shaped, the straight proximal border with three or four short conspicuous denticles, each of which may be bifid

terminally. Peristome scarcely developed, forming at the most a low rim around the distal and lateral borders of the orifice; three or four short distal oral spines present. Adventitious avicularium median suboral, cystid frequently columnar; mandible short, semi-elliptical, typically directed transversely. Vicarious avicularia sparsely developed, mandible narrowly spatulate, or subtriangular. Ovicell prominent, oval, overarching much of the primary orifice; thinly calcified, with a wide triangular frontal orifice.

Remarks

Celleporaria tridenticulata has been widely reported in the Indo-West-Pacific region, from the Great Barrier Reef and New Guinea to Ceylon and Mauritius. This is the first record of its occurrence in South African waters.

Celleporaria capensis (O'Donoghue & De Watteville, 1935)

Fig. 15I–J

Holoporella capensis O'Donoghue & De Watteville, 1935: 203, pl. 5 (figs 9–10), pl. 6 (fig. 15).

Material

Stations SM 163, SM 163/164, SM 180, SM 185.

Description

Colony encrusting, developing multilaminar sheets and nodules. Zooids oval, convex, thinly calcified; frontal calcification finely granular, translucent, with a few inconspicuous marginal pores. Orifice large, subterminal, wider than long, almost semicircular, proximal border slightly concave; two short and thick, widely spaced, distal oral spines present in young zooids. Peristome, when developed, forming simply a thin raised proximal lip, occasionally overarching the orifice in older zooids; rarely, peaked medially to form a short columnar umbo. Adventitious avicularia proximolateral to orifice, mandible elongate, semi-elliptical, directed distally; one or two present in newly budded zooids, later proliferating. Vicarious avicularia sporadically developed, mandible elongate, semi-elliptical or slightly spatulate. No complete ovicells found.

Remarks

C. capensis is known only from South Africa. Described originally from Still Bay, southern Cape (O'Donoghue & De Watteville 1935), it was subsequently reported from St. James and Oudekraal, south-western Cape (O'Donoghue & De Watteville 1937), and from Port Elizabeth (O'Donoghue & De Watteville 1944).

Family **Vittaticellidae** Harmer, 1957

Vittaticellidae Harmer, 1957: 765. Wass & Yoo, 1975: 286.

Vittaticella sp.

Fig. 11D

Material

Station SM 185.

Description

Zooids slender, clavate; small, less than 0,4 mm long, including proximal node, daughter zooid of doubleton scarcely smaller than the mother zooid. Primary orifice D-shaped, proximal border gently concave, a distinct lip proximally. Frontal wall smooth, with scattered, minute, pores; vittae elongate, narrow, extending from a point well proximal to the orifice, to close to the proximal end of the zooid, each with a well-marked series of pores on each side. Scapular chambers developed as prominent paired avicularia, with short semicircular mandibles; usually symmetrical, except in daughter zooids in which the inner, axial, avicularium is not developed. Suprascapular and infrascapular chambers very small, closely united with avicularium and not conspicuous. Ovicell not observed.

Remarks

The material was scanty, comprising part of a single small colony, and insufficient for a more detailed morphological study. From its general features this species seems to belong to the same group of species as the Indo-West-Pacific *V. tenella* Harmer, *V. venusta* (MacGillivray), and *V. praetenuis* (MacGillivray) (Harmer 1957: 776; Wass & Yoo 1975: 295), and could not be readily identified with any species known from the South African region. However, the vittaticellid fauna of the western Indian Ocean is poorly known.

Family **Mamilloporidae** Canu & Bassler, 1927

Mamilloporidae Canu & Bassler, 1927: 9. Harmer, 1957: 887.

Anoteropora Canu & Bassler, 1927

Anoteropora Canu & Bassler, 1927: 10. Harmer, 1957: 888.

Anoteropora latirostris Silén, 1947

Anoteropora latirostris Silén, 1947: 58, Pl. 5 (figs 25–27), figs 49–50. Hayward & Cook, 1979: 103.

Material

Stations SM 163/164, SM 185.

Description

Colony lunulitiform, large (up to 16 mm diameter), attached to sandy sediments by numerous basal rhizoids with deep vertical walls; frontal shield

small, with an almost central orifice. Both autozooids and brooding zooids with a large lateral avicularium, with curved, acute mandible.

Remarks

Eight complete colonies and fragments of several others were collected. Two of the five colonies from station SM 185 were alive at the time of collection and have intact basal rhizoids.

Distribution

Indo-West-Pacific.

ORDER CYCLOSTOMATA

Fragments of numerous species of Cyclostomata were present in the bottom sediments of most of the stations reported upon here, and were especially abundant in those from SM 163/164 and SM 129. Many of the specimens were of dead and worn colonies, evidently transported, including species of *Hornera*, *Tubulipora*, and *?Tervia*. The free tubular parts of peristomes and the brooding gonozooids are absent or damaged in most specimens rendering identification difficult. Although at least 20 distinct colony growth forms may be recognized, only 16 taxa have been identified, often doubtfully, to genus or species level. More than 40 species of cyclostomata have been reported from the South African region by Busk (1867, 1875, 1886), O'Donoghue (1924), O'Donoghue & De Watteville (1935, 1944) and Brood (1976*b*). Of these only 9 species have been found in the present *Meiring Naude* collections, although 1 additional form, *Crisia* aff. *holdsworthii*, was listed by Hayward & Cook (1979: 116). One notable absentee is *Tennysonia stellata* Busk (1867: 242, pl. 36 (figs 10–11)), which was first reported from South Africa, and has large, robust colonies. Another South African species, *Disporella buski* Harmer (1915: 161, pl. 12 (figs 4–5)), is known to have a wide distribution but is also absent from the present collections.

Generally, nominal species, at least, have very wide distributions and some species have been identified, both here and by Brood (1976*b*), with forms reported from the Philippines by Canu & Bassler (1929), from Indonesia by Harmer (1915), and from Australia by MacGillivray (1885). Examination of the type suites of some species, for example those described by Busk (1875, 1886) in the British Museum Catalogue and the *Challenger* Report respectively, has revealed, however, a wide range of variation within populations of nominal species. Some of these variants may even prove to be specifically distinct. It is obvious that revision of the South African cyclostome fauna will require detailed analysis of well-preserved, preferably living, colonies. Harmelin (1976*b*) has demonstrated that within the Mediterranean Tubuliporina many colony forms, and even zooid morphologies, are radically modified by environmental influences, and that convergence of character states can occur

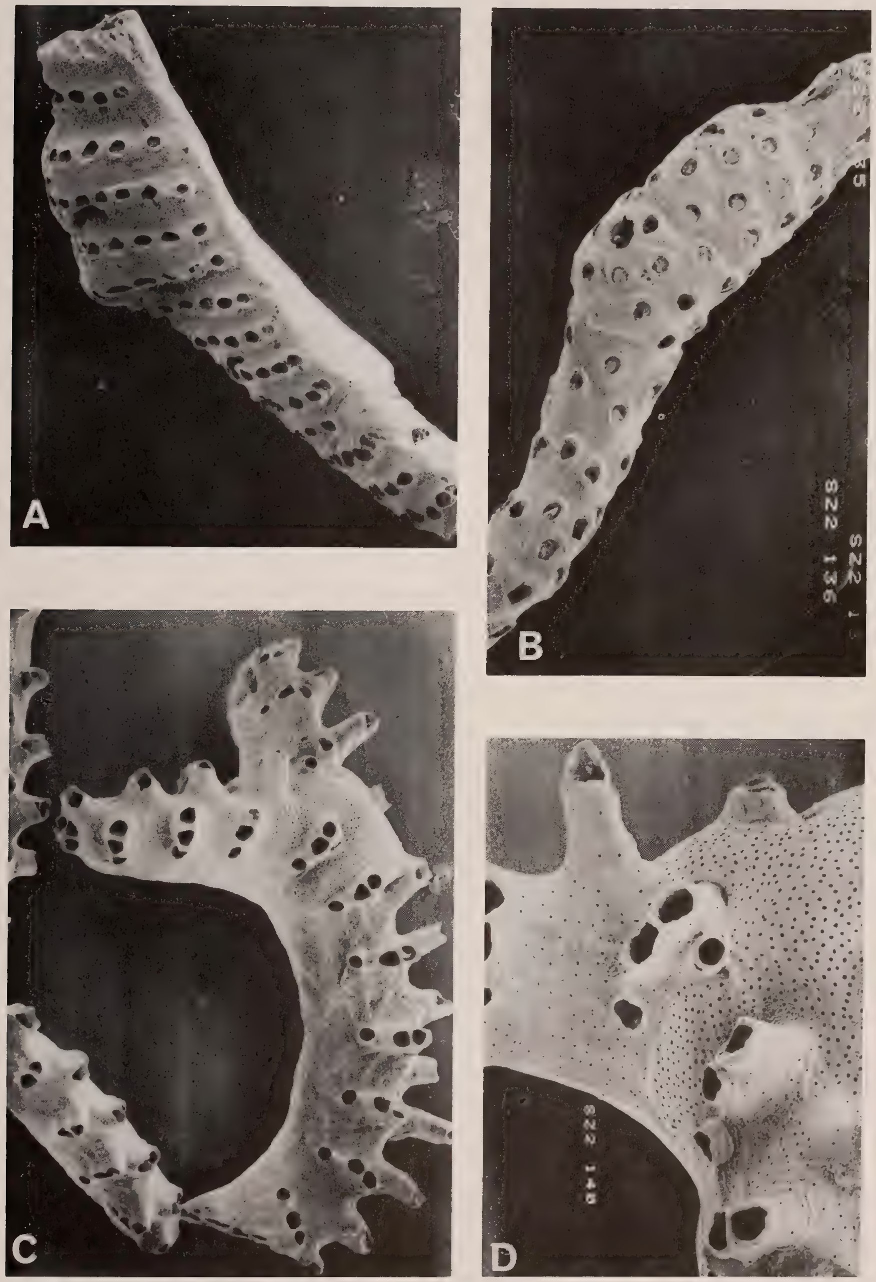

Fig. 32. A. *Idmidronea contorta* (Busk). × 16. B. *Mecynoecia clavaeformis* (Busk). × 17. C–D. *Idmidronea crassimargo* (Canu & Bassler). C. Two fragments of a colony, including a gonoecium. × 26,3. D. Detail to show ooeciostome. × 62.

among systematically unrelated species. Until such a detailed study may be made, it is pointless to attempt to revise specific and generic concepts, or to assign very worn fragments to previously described species. In assigning the present material to particular species it is not implied that the specimens have been compared with type material, unless so stated; rather, it is considered that the *Meiring Naude* fragments closely resemble the specimens illustrated by the authors listed in the synonymies.

Family **Diaperoeciidae** Canu, 1918

Diaperoeciidae Canu, 1918: 329.

Diaperoecia Canu, 1918

Diaperoecia Canu, 1918: 329. Harmelin, 1976*b*: 78.

Diaperoecia sp.

Material

Station SM 163.

Remarks

A single colony, lacking gonozooids, was found encrusting a worn, erect cheilostome bryozoan.

Family **Entalophoridae** Reuss, 1869

Entalophoridae Reuss, 1869: 285.

Mecynoecia Canu, 1918

Mecynoecia Canu, 1918: 326. Harmelin, 1976*b*: 160.

The characters of the genera *Pustulopora* and *Mecynoecia* have been discussed by Brood (1976*a*, 1976*b*) and Harmelin (1976*b*).

Mecynoecia clavaeformis (Busk, 1875)

Fig. 32B

Pustulopora clavaeformis Busk, 1875: 22, pl. 14 (figs 1–4).

Material

Stations SM 131, SM 163/164.

Description

Colonies club-shaped, up to 20 mm high, arising from a small, encrusting base. Zooids in irregular closely spaced whorls of three to six.

Remarks

Although somewhat worn, the fragments agree exactly with the material from Algoa Bay (BMNH 1875.5.29.34, 1899.7.1.530) described by Busk (1875).

Busk's specimens were also fragmentary and provide little information as to the later growth form of the colony and the systematic relationships of the species.

Mecynoecia delicatula (Busk, 1875)

Pustulopora delicatula Busk, 1875: 21, pl. 6B (fig. 3). Brood, 1976*b*: 290, fig. 13E–F.
Mecynoecia delicatula: Harmelin, 1976*b*: 160, pl. 27 (figs 1–8).

Material

Stations SM 129, SM 163/164, SM 185.

Description

Colonies erect, occasionally branched, with long zooids opening irregularly on all sides. Free peristomes long and curved. Gonozooids often at bifurcations, simple.

Remarks

Most specimens were slightly worn, and lacked the long peristomes. Brood (1976*b*) noted that this species was common from 50 to 700 m in east African waters.

Mecynoecia australis (Busk, 1852)

Pustulopora australis Busk, 1852: 350; 1875: 21, pl. 17A. Brood, 1976*b*: 291, fig. 13A.
Pustulopora proboscidea: Busk, 1886: 19, pl. 4 (fig. 2).

Material

Stations SM 129, SM 151, SM 163/164, SM 180, SM 185.

Description

Colonies similar to those of *M. delicatula* but with larger zooids and coarser calcification.

Remarks

Brood (1976*b*) reported *M. australis* as rare in east African waters, with a bathymetric range of 75 to 700 m.

Distribution

Indo-Pacific.

Family **Diastoporidae** Busk, 1859

Diastoporidae Busk, 1859: 91, 113. Harmelin, 1976*b*: 119.

Plagioecia Canu, 1918

Plagioecia Canu, 1918: 327. Harmelin, 1976*b*: 128.

Plagioecia patina (Lamarck, 1816)

Tubulipora patina Lamarck, 1816: 163.
Plagioecia patina: Harmelin, 1976*b*: 129, pl. 8 (figs 5–9), pl. 18 (figs 4–9), pl. 19 (figs 1–5).

Material

Station SM 163/164.

Description

Colonies forming flattened discs, often with an extended peripheral lamina and small subcolonies. Early budding fan-shaped, later zooids in repent, connate, single, radial rows. Gonozooids peripheral, transversely extended, ooeciostomes central.

Remarks

Two colonies were found, one of which was alive when collected.

Distribution

Temperate Atlantic, Mediterranean, and eastern Pacific.

Liripora MacGillivray, 1887

Liripora MacGillivray, 1887: 182.
Desmeplagioecia Canu & Bassler, 1920: 718. Brood, 1976*b*: 284.

MacGillivray (1887) introduced *Liripora* for two Recent Australian species, *L. lineata* (see below) and *L. fasciculata*, both of which had been originally assigned to *Diastopora* in an earlier paper (MacGillivray 1885). *L. fasciculata*, together with several fossil species included in the genus by MacGillivray (1895), is probably generically distinct from *L. lineata*. However, as the first species described in 1885 and the first listed in 1887, *L. lineata* may be regarded as the type species of *Liripora*, and Canu & Bassler (1920) seem to have introduced *Desmeplagioecia*, for *D. lineata*, unnecessarily. Canu (1908: 310) used the name *Liripora* incorrectly for flabellate species of *Tubulipora*.

Liripora is obviously closely related to *Plagioecia*, being distinguished principally by its multiple radial rows of connate zooids. The genus is also very similar to the fossil *Actinopora* d'Orbigny (see Brood 1976*b*: 284).

Liripora lineata (MacGillivray, 1885)

Diastopora lineata MacGillivray, 1885: 96, pl. 3.
Liripora lineata: MacGillivray, 1887: 182.
Berenicea lineata: Harmer, 1915: 116, pl. 11 (figs 6–7).
Desmeplagioecia lineata: Canu & Bassler, 1920: 718, fig. 234. Brood, 1976*b*: 284.

Material

Stations SM 163/164, SM 185.

Description

Colony encrusting, discoid, with a basal lamina; forming subcolonies by frontal extension. Primary zooids repent, budding distally and laterally. Later zooids radially disposed; peristomes connate, raised terminally, becoming

multizooidal. Areas between zooid rows calcified but not reticulate. Gonozooids peripheral and subperipheral, with distal ooeciostomes.

Remarks

Three young colonies, and a single group of four subcolonies were found; all were alive when collected. One further colony, on the concave side of a lamellibranch shell, had three gonozooids, and was dead. The subcolonies are formed by frontal extension of one or more peripheral zooids of the mother colony, which forms a new basal lamina. Some of the Australian colonies examined (BMNH 1897.5.1.1377, 1963.2.12.19.) are more robust than those from South Africa, but others are almost exactly the same in all characters.

A similar species, *Diastopora reticulata*, described from the Antarctic by Borg (1944: 68, pl. 4 (figs 3–8)), has reticulate interzooidal areas and a tubular ooeciostome.

Distribution

Indo-Pacific, including Japan and Australia.

Family **Tubuliporidae** Johnston, 1838

Tubuliporidae Johnston, 1838: 247. Harmelin, 1976*b*: 165.

Idmidronea Canu & Bassler, 1920

Idmidronea Canu & Bassler, 1920: 784. Harmelin, 1976*b*: 181. Buge, 1979: 232.

Harmelin (1976) discussed the character of *Idmidronea* and related genera, and noted the difficulties in distinguishing species, due to environmentally induced variation between populations of single species. Six different kinds of colony belonging to *Idmidronea* were distinguished in the *Meiring Naude* collections. Although these have been identified with known species, it should be noted that several of these were originally described from one or two fragments only, which may have represented parts of a single, variable species.

Idmidronea contorta (Busk, 1875)

Fig. 32A

Idmonea contorta Busk, 1875: 12, pl. 8. O'Donoghue, 1924: 24.
Tennysonia contorta: Canu & Bassler, 1922: 52, pl. 11 (figs 11–14); as *Lobosoecia semiclausa*, in error, on p. 145.

Material

Stations SM 129, SM 131, SM 163/164, SM 185.

Description

Branches short, inflated, curved; flat basally. Zooids connate, in alternating groups of six. Gonozooids occurring at bifurcations.

Remarks

The fragmentary specimens are closely similar to those from Algoa Bay described by Busk (BMNH 1875.5.29.18). The gonozooid has not been described before, but the specimens are worn and the ooeciostome is not obvious. *I. contorta* was recorded by O'Donoghue (1924) from several South African localities, from depths of 55–169 m. Harmelin (1976*b*) noted that Mediterranean records of this species are referable to *Tubulipora notomale* Busk (1875), which has much larger zooids.

Idmidronea crassimargo (Canu & Bassler, 1929)

Fig. 32C–D

Idmonea crassimargo Canu & Bassler, 1929: 545, pl. 85 (figs 2–3).
Idmidronea crassimargo: Brood, 1976*b*: 290, fig. 5I–J, M.

Material

Stations SM 163/164, SM 185.

Description

Colonies with basal side of branches curved, zooids in alternating, connate groups of three. Gonozooid short, inflated, frequently placed at a bifurcation; ooeciostome small, rounded with a short tube, central or lateral.

Remarks

Originally described from the Philippine Islands, from 320 m, this species was also recorded from several east African localities by Brood (1976*b*) between 60–150 m. Several of the *Meiring Naude* specimens were alive when collected; the gonozooids have not been figured before.

Idmidronea cf. *parvula* (Canu & Bassler, 1929)

Fig. 33A

Idmonea parvula Canu & Bassler, 1929: 546, pl. 85 (fig. 1).

Material

Stations SM 163/164, SM 185.

Description

Branches with flat basal side. Zooids in alternating connate groups of two or three.

Remarks

Several fragments of this small species were found, two of which had incomplete zigzag gonozooids. The zooids are distinctly smaller than those of *I. crassimargo*, and larger than those of *I.* cf. *biporata* (below). The gonozooids

Fig. 33. A. *Idmidronea* c.f. *parvula* (Canu & Bassler). × 24. B–D. *Hornera erugata* sp. nov. B. Frontal view of a branch, including a gonoecium. × 26,7. C. Detail to show ooeciostome. × 50. D. Basal view of colony and gonoecium. × 17,8.

are not inflated like those of *I. biporata*, but it is possible that all of these small forms, including *I.* cf. *antarctica* (below) are either very closely related systematically, or represent ecologically varying populations of the same species.

Idmidronea cf. *biporata* Brood, 1976

Idmidronea biporata Brood, 1976*b*: 290, fig. 5F–H.

Material

Stations SM 163/164, SM 185.

Description

Zooids very small, in alternating pairs, gonozooids inflated.

Remarks

Only three fragments were found. the zooids are minute, even smaller than those figured by Brood (1976*b*).

Idmidronea cf. *antarctica* Borg, 1944

Idmidronea antarctica Borg, 1944: 84, pl. 6, (fig. 4), pl. 7 (figs 1–2).

Material

Stations SM 129, SM 131, SM 163/164.

Description

Branches flat basally; zooids in closely spaced, alternating, connate groups of five. Gonozooids forming a zigzag ridge frontally.

Remarks

Only four minute fragments were found. The zooids are smaller than those figured by Borg (1944), but the gonozooid closely resembles that of *I. antarctica*, which also has five zooids in each group.

Idmidronea cf. *atlantica* (Forbes in Johnston, 1847)

Idmonea atlantica Forbes in Johnston, 1847: 278.
Idmidronea atlantica: Harmelin, 1976*b*: 182, pl. 32 (figs 1–11). Hayward & Cook, 1979: 116. Buge, 1979: 232, pl. 7 (fig. 4).

Material

Stations SM 129, SM 163/164.

Remarks

Numerous worn fragments were found, none of which had complete gonozooids. They are provisionally assigned to this widely distributed and very variable species.

Family **Crisiidae** Johnston, 1847

Crisiidae Johnston, 1847: 282.

Crisia Lamouroux, 1812

Crisia Lamouroux, 1812: 183. Ryland, 1967: 272.

Crisia elongata Milne Edwards, 1838

Crisia elongata Milne Edwards, 1838: 203, 235, pl. 7 (fig. 2). Busk, 1875: 5, pl. 4 (figs 5–6). Harmer, 1915: 103, pl. 8 (figs 13–17). Brood, 1976*b*: 282, fig. 4F, J, N.

Material

Stations SM 123, SM 163/164.

Description

Colonies with elongated, almost straight internodes, consisting of ten to twenty alternating zooids. Peristomes curved forward, short. Basis rami short, wedged in between two zooids, branches usually occurring high in an internode. Gonozooid dilated distally, ooeciostome slit-like, without a raised rim. Joints black.

Remarks

The material comprised numerous well-developed living colonies with extensive kenozooidal rooting systems. The joints are dark yellow early in ontogeny, rapidly becoming black. No gonozooids were present. The colonies are slightly less robust than Busk's colonies from Algoa Bay (BMNH 1875.5.29.5), but are closely similar to Brood's (1976*b*) figures of east African material. *C. elongata* differs from *C. transversata* Brood (1976*b*: 282, fig. 4E, G–I), which also has black joints, in having shorter zooids, longer and straighter internodes, less prominent peristomes and a longer gonozooid. *C. holdsworthii* Busk, which was reported from the earlier *Meiring Naude* collections, has much longer, more delicate zooids, and relatively colourless joints.

Distribution

Indo-Pacific, including Japan and Australia.

Family ***Lichenoporidae*** Smitt, 1866

Lichenoporidae Smitt, 1866: 404, 474.

Lichenopora Defrance, 1823

Lichenopora Defrance, 1823: 257.

Lichenopora novae-zealandiae (Busk, 1875)

Discoporella novae-zealandiae Busk, 1875: 32, pl. 30 (fig. 2).
Lichenopora novae-zealandiae: Harmer, 1915: 155, pl. 12 (figs 6–11). Brood, 1976*b*: 299, fig. 17H–I.

Material

Stations SM 131, SM 163/164, SM 184, SM 185.

Description

Colonies discoidal, raised centrally, with almost vertical sides. Zooids in radial, connate rows, the ends of the peristomes not free. Gonozooids central, surrounded by extrazooidal calcification; ooeciostomes large, rounded.

Remarks

Sixteen colonies were found, five of which were alive when collected. *L. novae-zealandiae* differs from *Disporella buski* Harmer, originally described (as *D. ciliata* Busk, 1875) from the Cape of Good Hope, in its regularly radial, connate zooid series, which are not free terminally (see Brood 1976*b*: 299, fig. 17D–G; Buge 1979: 242, pl. 9 (fig. 1)).

Distribution

Indo-Pacific, including Japan, Australia and New Zealand.

Family **Crisinidae** d'Orbigny, 1853

Crisinidae d'Orbigny, 1853: 902. Borg, 1941: 35.

Crisina d'Orbigny, 1850

Crisina d'Orbigny, 1850: 265; 1853: 912. Borg, 1941: 2.

Crisina radians (Lamarck, 1816)

Retepora radians Lamarck, 1816: 183.
Crisina watersi Borg, 1941: 16, pl. 2 (figs 3–4), pls 3–4.
Crisina radians: Brood, 1976*b*: 297, fig. 15H–J.

Material

Station SM 131.

Description

Colonies profusely and regularly branched in one plane; basal surface of branches flat, composed of kenozooids. Zooids in alternating connate groups of three to four.

Remarks

Two bifurcating fragments were found, one of which bore a gonozooid. Brood (1976*b*) considered that the east African material described as *C. watersi* by Borg (1941) was within the range of variability displayed by *C. radians*.

Distribution

Crisina radians is widely distributed in the Indo-West-Pacific region, from east Africa to Australasia, and also in New Zealand waters.

Family **Horneridae** Smitt, 1866

Horneridae Smitt, 1866: 404, 465. Gregory, 1899: 360. Borg, 1926: 385.

Hornera Lamouroux, 1821

Hornera Lamouroux, 1821: 41. Harmer, 1915: 147. Borg, 1926: 204, 385.

Hornera erugata sp. nov.

Fig. 33B–D

Hornera sp. Cook, 1968: 238.

Material

Holotype: BMNH 1842.11.30.45, Cape of Good Hope.
Paratypes: SAM–A26456, as above, Cape of Good Hope.
Other material: station SM 163.

Description

Colony erect, branching; branches curved in more than one plane. Zooids in laterally contiguous series of three to seven; peristomes long, often bifurcate in lateral zooids. Secondary branches formed by fascicles of three to four zooids. Basal extrazooidal calcification smooth, without obvious pores. Gonozooid basal, surface smooth; ooeciostome large, slit-like, lateral, closely opposed to the side of the branch, without a raised rim.

Etymology

Erugatus (L.)—smooth, referring to the basal calcification.

Remarks

Of the numerous worn fragments of *Hornera* present in the *Meiring Naude* bottom samples (p. 142), only three, relatively unworn, had the smooth basal calcification of *H. erugata*. The basal calcification of other species of *Hornera* is invariably corrugated, with large pores, pits and intervening ridges. The lack of corrugations on the gonozooid of this species is also unusual, as is the absence of a rim to the ooeciostome.

A somewhat similar species, which has ridged, porous basal calcification and a reticulate gonozooid with a raised, lateral ooeciostome, was described from the Antarctic as *H. smitti* by Borg (1944: 199, pl. 15 (figs 2–8)). *Pseudidmonea gracilis* Androsova (1965: 80, fig. 18), another Antarctic species, has a gonozooid somewhat like that of *H. erugata*, but a more delicate colony, with alternating series of three to five connate zooids.

Measurements (range of 10 values) in mm

Lz	Lg	lg	Loo.st.
0,4–0,5	2,5–3,0	2,0–2,5	0,4–0,55

DISCUSSION

General review of collection

The particular importance of the material described in the preceding account derives from the fact that it was collected from a range of depths for the most part far shallower than those from which the first series (1975–6) of *Meiring Naude* samples was taken. The bryozoan collections from the first two cruises originated from stations further to the north and east than those of subsequent cruises, and could be characterized largely as typical continental slope assemblages (Hayward & Cook 1979). The present collections are from a number of stations established off-shore between Durban and East London, the majority of which were located on the continental shelf of this region. Thus, 9 of the samples reported upon here were collected from depths of less than 200 m, 6 range between 500 m and 700 m, and only 3, 1 of which (SM 103) represents a residue from the 1976 cruise, were obtained from depths in excess of 700 m. The greatest depth sampled for bryozoans in the later survey was station SM 151, at 900 m. By contrast, the greatest depth represented in the first series of samples (Hayward & Cook 1979) was 1 300 m, with the majority of the material originating from between 600 m and 1 000 m. It is not surprising, then, that the bryozoan faunas revealed in each case should differ markedly.

The first report described 51 species, 48 of which were cheilostomata; the number of anascan species was only a little smaller than the number of ascophora and included several which were considered to be particularly adapted to life on the fine, unconsolidated sediments of the continental slope, such as the small colonies of *Setosellina*, *Heliodoma* and *Inversiscaphos*. There were also representatives of cellularine genera, for example *Columnella*, *Notoplites*, and *Bugulella*, frequently associated with slope faunas. The ascophora, similarly, included a number of highly specialized species in the genera *Anoteropora*, *Batopora* and *Lacrimula*. The present collection offers an immediate contrast in both the total number of taxa recorded, 130, and in the increased proportion of ascophorans. There were almost twice as many ascophorans (Table 2) as anascans (Table 1), and these were predominantly encrusting forms, together with a significant proportion with erect, rigid colonies, most notably the species of *Adeonella*. The anascans included a range of encrusting species, and a number of cellularines, such as *Menipea*, typically associated with shallow water faunas. A further difference is seen in the substantial number (sixteen) of Cyclostomata identified in these samples; with two exceptions (Table 3) live specimens of cyclostome species were recorded only at stations with depths of less than 100 m.

Only twenty-two of the species described here had been reported in the first *Meiring Naude* collections. For the most part these comprised species which occurred only at stations deeper than 500 m (e.g. *Tessaradoma* spp.), or which were represented in the first collections by specimens from the shallowest

stations only (e.g. *Flustramorpha angusta*, *Reteporella dinotorhynchus*), or which appear to have very broad bathymetric distribution patterns (*Setosellina roulei*). Thus, the two collections complement each other most usefully, and together provide a representative survey of the shelf and slope faunas of eastern South Africa. The results of the *Meiring Naude* cruises, together with the accounts published in the century following the *Challenger* investigations, provide a sound base line for future research on the bryozoan fauna of this region.

Including the new species described here, more than 280 nominal forms of Bryozoa have been reported from South Africa. Descriptions of these may be found in Busk (1852, 1854, 1884), Marcus (1922), Harmer (1926, 1934, 1957), the papers of O'Donoghue and O'Donoghue & De Watteville (q.v.), and a very few other sources. A precise enumeration is not yet possible, largely through outstanding problems of synonymy. Many South African forms were originally assigned the names of European species and, while it has been possible to review the systematic status of some of these, others will perhaps never be recognized. O'Donoghue (1924), for example, noted that both *Cellaria fistulosa* (Linnaeus) and '*Lepralia*' *foliacea* (Ellis & Solander) had been reported from South Africa, yet in view of the known geographical distribution of these two species (Ryland & Hayward 1977; Hayward & Ryland 1979) this seems improbable, and there is no way of ascertaining to which species these names were applied. Despite such problems, some useful synonymizing has been achieved by previous authors. *Caberea boryi* (Audouin), listed by Busk (1852) from Algoa Bay, may now be recognized as *C. darwinii* Busk (O'Donoghue 1924), and all records of *Steginoporella magnilabris* (Busk) may be assigned to *S. buskii* Harmer (O'Donoghue 1957). Several names introduced for South African bryozoans have proved to be junior synonyms of previously described species; for example *Bicellariella capensis* O'Donoghue is *B. chuakensis* Waters (O'Donoghue 1957), and *Beania paucispinosa* O'Donoghue & De Watteville is *B. vanhoffeni* Kluge (O'Donoghue 1957).

Research on the *Meiring Naude* samples has allowed some opportunity for revision and reassessment of previously known species. For example, Hasenbank's (1932) record of *Beania erecta* Waters is here redescribed as *B. rediviva* sp. nov. However, although it is clear that much similar revisionary work remains to be done, only 51 of the species described in this report have been described before from South African waters; with the exception of *B. rediviva*, the rest are either new species or newly reported for the region. For the slope fauna (Hayward & Cook 1979) 44 out of a total of 51 species belonged to these latter two categories. Thus, the bryozoan fauna of both the shelf and slope of eastern South Africa has a far greater diversity than was hitherto suspected and it is probable, from evidence discussed below, that its complete diversity is as yet uncharted. The fauna now known has a taxonomic diversity comparable to those of other, more widely studied, areas of continental shelf seas. For example, Cook (1983*b*) has listed 222 species from the shelf waters of west

Africa, and the cheilostome fauna of the British sea area (Ryland & Hayward 1977; Hayward & Ryland 1979) totals 186 species. The *Meiring Naude* investigations revealed a very high proportion of formerly undescribed cheilostomata which, together with the considerable numbers of apparently rare species also collected, suggests that the eastern South African fauna includes a substantial endemic element. It is likely that further surveys, with a coverage as intense as that accomplished by Millard (1975, 1978) for the hydroids, encompassing the whole of southern Africa will greatly enhance the presently known diversity of bryozoan species.

Analysis of bottom deposits

Two immediate impressions are gained from initial examination of the abundant sediment samples collected from a number of the *Meiring Naude* stations. Firstly, there is an almost complete absence of the minute 'sand fauna' species discussed in the previous report (Hayward & Cook 1979); secondly, a high proportion of the sediment at some stations consists of bryozoan skeletal remains.

The reasons for the virtual absence of such genera as *Batopora*, *Lacrimula* and *Heliodoma*, which were so abundant in the samples from stations SM 16–SM 109 (see Hayward & Cook 1979) are not obvious, and do not appear to be related directly to depth. These specialized forms were found in the first series of samples from depths of 376 to 1 300 m. Samples from similar depths were included in the present collections, yet *H. implicata* was frequent only in the residue of station SM 103, and none of the ascophoran genera, with the exception of *Anoteropora*, were found. The range of sediment particle size seemed essentially very similar in both series of samples, and although, as stated above, the stations of the 1977–9 surveys were situated further south than those of the 1975–6 cruises, other environmental parameters, such as bottom temperature, appear to have the same range with depth in both collections (Louw 1977, 1980).

An analysis of sediment types for ten stations for which samples were available is given in Table 4. The data comprise the approximate proportions of different constituents in a single sample for each station, graded in three coarse size fractions. The number of bryozoan species identified is given for each station including the number present as dead material only. There is considerable variation in sediment size between stations; for example, for SM 184 40 per cent of the sample was retained by the 5 mm sieve, while nothing passed the 1 mm sieve, whereas for SM 185 48 per cent of the sample passed the 1 mm sieve and nothing was retained by the 5 mm sieve. Inspection of the table reveals no apparent correlation between bryozoan diversity and sediment size.

The proportion of biogenic sediments in each size fraction also varies widely from station to station and again suggests no correlation with bryozoan diversity. Shell fragments constituted from 10 to 50 per cent of each sample,

often in the two smaller size fractions; these were largely finely comminuted molluscan shell, although remains of echinoderm test were frequent, and the coarsest fragments often included a significant proportion of decapod shell. The most interesting feature of this table is the significant contribution to the sediment made by bryozoan skeletal remains at several stations, viz. SM 129, SM 131, SM 151, SM 163/164, SM 179. At SM 179, in particular, bryozoan remains comprised 50 per cent of the sample. Most of the fragments were of erect genera, such as the cheilostomes *Flustramorpha*, *Adeonella* and *Sertella*, and the cyclostomes *Mecynoecia*, *Idmidronea* and *Hornera*. Three subsamples from station SM 163/164, each of 1 cm^3 volume when dried, were studied in greater detail; an average of 400 bryozoan fragments was found per sample, of which 25 per cent were cyclostomata and 75 per cent cheilostomata. The total sediment sample for this station was estimated to contain 18 000 bryozoan fragments; 56 species were recorded for this station, including 24 that were represented by dead fragments only. The high species diversity and abundance of bryozoans in this region is thus reflected in the constitution of the bottom deposits; similar results were found by Wass *et al*. (1970) in a study of the Southern Australian shelf and slope. However, Table 4 also emphasizes the problems encountered in attempting to describe patterns of geographical and bathymetric distribution, and the need to differentiate carefully between living and dead, or attached and loose, specimens in benthic samples. A number of the species described above were represented by dead material only, and their real distribution remains unknown. The proportion of species represented by dead specimens only increases with depth; the stations in Table 4 with a high content of bryozoan remains in the sediment range in depth from 80 m (SM 179) to 850 m (SM 129). It is likely that each includes a different proportion of transported material while none probably represents a true thanatocoenosis. The proportion of very worn material varied from station to station; for example, 30 per cent of the skeletal material from SM 163/164 was too abraded to be identified, and 70 per cent of that at SM 179 was similarly unidentifiable. While some specimens could not even be readily assigned to a family grouping, others could be recognized as species, or even genera, which were not otherwise recorded in these collections, but which could not be reliably characterized. For example, abraded internodes of a species of *Margaretta* were frequent in several of the sediment samples. The last three stations in Table 4 (SM 180, SM 184, SM 185) each had a high diversity of bryozoan species, including a significant proportion of dead material, yet bryozoan skeletal remains were negligible in, or absent from, the sediments from these stations. In these three cases the living material included several cellularine species and a substantial number of large erect species (*Adeonella*, *Gigantopora*) encrusted with numerous other cheilostomata. Although the removal of large dead fragments from these samples prior to analysis undoubtedly biases the results, the lack of finer skeletal remains and the predominance of erect branching species probably reflect

local hydrographic conditions which are not conducive to the accumulation of bryozoan deposits.

Colonies of *Dactylostega prima* and *Chaperia familiaris*, particularly from stations SM 162 and SM 180, were often frequent on the tests of large specimens of the rhizopod foraminiferan *Schizammina pinnata* (Pearcey). This foraminiferan is known only from the south-eastern coast of South Africa (between 57 and 228 m), where it is frequently, although sporadically, abundant. The family Schizamminidae was introduced by Nørvang (1961) for

TABLE 4

Analysis of sediment components (%) from ten *Meiring Naude* stations. A = < 1 mm fraction; B = 1–5 mm fraction; C = > 5 mm fraction; T = terrigenous material; S = shell; FS = foraminiferans with sand accreted tests; FC = foraminiferans with calcareous tests; BR = bryozoan fragments.

Station	Depth m		T	S	FS	FC	BR	Bryozoan spp. Total	Bryozoan spp. Dead
SM 103	680	A	20	0	50	0	0	7	6
		B	5	10	10	0	2		
		C	3	0	0	0	0		
SM 123	690	A	10	0	0	10	0	2	0
		B	0	10	0	20	0		
		C	10	10	10	20	0		
SM 129	850	A	25	5	2	3	0	7	7
		B	5	10	10	0	10		
		C	10	5	5	0	10		
SM 131	780	A	10	20	1	1	5	22	21
		B	0	25	1	0	25		
		C	2	5	0	0	5		
SM 151	900	A	0	5	5	0	5	8	8
		B	0	20	10	0	15		
		C	0	10	10	0	20		
SM 163/164	90	A	15	0	0	5	0	67	24
		B	0	20	0	5	30		
		C	0	10	0	0	15		
SM 179	80	A	5	5	0	0	10	24	4
		B	5	5	0	0	10		
		C	15	15	0	0	30		
SM 180	80	A	25	20	5	0	0	27	21
		B	20	20	5	5	0		
		C	0	0	0	0	0		
SM 184	86	A	0	0	0	0	0	23	12
		B	25	30	5	0	0		
		C	15	20	5	0	0		
SM 185	90	A	20	25	3	0	2	55	15
		B	20	25	3	0	2		
		C	0	0	0	0	0		

two genera of large Foraminifera, *Schizammina* and *Jullienella*, some species of which may grow to 70 mm in height or diameter, and which have dark or reddish-brown, rigid tests composed of agglutinated sand grains. *S. pinnata* (Nørvang, 1961: 192, pl. 7 (figs 9–17)) is robust, elongated, and has regularly alternating, short, sympodial branches, which form a zigzag pattern. Another South African species, *Jullienella pearceyi* Nørvang (1961: 198, pl. 9 (figs 1–11, 14)), is smaller, more inflated and almost polygonal in shape. In west African waters the large fimbriated plates of *J. foetida* Schlumberger (Nørvang, 1961: 195, pl. 8 (figs 1–13)) form the major substratum in some areas for a diverse fauna of bryozoan species (Cook 1968, 1983*b*). The mode of life of the foraminiferans is not known, but they are frequently covered on both surfaces by encrusting bryozoan colonies. Worn and fragmented specimens often form a significant proportion of bottom sediments (Table 4).

Geographical distributions

In Table 5 known geographical ranges are given for seventy-three previously described species. Fifty-one of these have been reported before from South Africa. The twenty-two species here recorded for the first time include a number which appear to have generally broad geographical distribution patterns, such as *Parasmittina tropica*, *Escharina pesanseris*, *Trypostega venusta*, *Celleporaria tridenticulata* and *Crisina radians*. Several others, such as *Cribrilaria innominata* and *Cleidochasma porcellanum*, are known to be complex variable entities in which apparently very broad distributions may be simply artefacts of systematic uncertainty. However, at least half of these twenty-two species are characterized by less broad distributions suggestive of more interesting patterns. *Hippoporidra senegambiensis* has an otherwise rather limited distribution on the west African shelf; *Cupuladria multispinata*, *Setosellina roulei*, *Heliodoma implicata*, and perhaps *Cribrilaria venusta* (p. 43) appear to show similarly narrow distributions, but in total these species constitute a minority in the eastern South African fauna. *Caberea darwinii* and *Brodiella longispinata* seem to be more widely distributed, cold-temperate Southern Hemisphere species, probably at the extreme northern limit of their range in South African waters. This pattern is seen in another species, *Amphiblestrum inermis*, long known from South Africa. However, the arrangement of Table 5 emphasizes the accepted faunal similarity of eastern South Africa with the Indo-West-Pacific realm and, like the previously reported species, these new records are predominantly of species with distributions extending through part or whole of this realm. *Escharina waiparaensis*, formerly known only from New Zealand, and *Hippomenella avicularis*, described from a few stations in the western Pacific, represent particularly significant range extensions; the distribution of *Hippoporella spinigera* is established through the inclusion in its synonymy of *Mucronella serratilabris* O'Donoghue (1924). *Crassimarginatella marginalis* seems to have a narrow

TABLE 5

Geographical distributions of previously described species.

	Atlantic	West Africa	South Africa	East Africa	Indian Ocean	Malay Archi-pelago	West Pacific	East Pacific	New Zealand	Sub-antarctic	Antarctic
Carbasea mediocris			×								
Cupuladria multispinata	×	×	×								
Discoporella umbellata	×	×	×	×							
Setosellina roulei	×		×								
Heliodoma implicata	×		×								
Amphiblestrum inermis			×								×
Crassimarginatella marginalis					×						
Foveolaria imbricata			×								
Chaperia multifida	?		×								
Chaperia capensis			×								
Chaperia stephensoni			×								
Notocoryne cervicornis			×								
Steginoporella buskii	×	×	×	×	×	×	×				
Cellaria tectiformis			×								
Cellaria punctata			×	×	×	×	×				
Cellaria paradoxa			×								
Caberea darwinii	×								×	×	×
Eupaxia quadrata			×	×	×						
Menipea crispa			×	×							
Menipea triseriata			×								
Menipea ornata			×								
Menipea marionensis			×								
Bugulella australis			×				×				
Beania magellanica	×	×	×		×		×		×	×	
Bugula dentata		×	×		×	×	×				
Cribrilaria innominata	×						×				
Cribrilaria venusta	×	×									
Figularia philomela			×		×						
Escharoides contorta			×								
Pachycleithonia mutabilis					×	×	×				
Tropidozoum burrowsi			×		×						
Parasmittina tropica		×		×	×	×	×				
Porella capensis			×								
Arthropoma cecilii	×	×	×	×	×	×	×				
Arthropoma circinatum	×						×	×	×		
Escharina pesanseris	×	×		×	×	×	×				
Escharina waiparaensis									×		
Calyptotheca nivea			×								
Calyptotheca porelliformis			×								
Stomachetosella balani			×								
Cleidochasma porcellanum	×	×		×	×	×	×				
Cleidochasma protrusum			×	×	×	×	×				
Cleidochasma cribritheca			×								
Hippoporidra senegambiensis		×									
Hippoporella spinigera			×			×	×				
Hippomenella avicularis							×				
Flustramorpha flabellaris			×								
Flustramorpha marginata			×		×						
Flustramorpha angusta			×								
Trypostega venusta	×	×		×	×	×	×	×	×		
Gigantopora polymorpha			×								
Adeonella majuscula			×								
Adeonella cracens			×								
Tessaradoma bispiramina			×								
Tessaradoma circella			×								
Sertella lata			×								
Schizoretepora tessellata			×				×				
Reteporella dinotorhynchus			×								
Brodiella longispinata	×								×		
Turbicellepora conica			×								
Celleporaria tridenticulata					×	×	×	×	×		
Celleporaria capensis			×								
Anoteropora latirostris			×	×	×	×					
Mecynoecia clavaeformis			×								
Mecynoecia delicatula				×							
Mecynoecia australis				×							
Plagioecia patina	×	×						×			
Liripora lineata				×		×	×				
Idmidronea contorta			×								
Idmidronea crassimargo				×			×				
Crisia elongata			×	×	×	×	×				
Lichenopora novae-zealandiae				×	×	×	×	×	×		
Crisina radians				×	×	×	×		×		

distribution within the Indian Ocean and is of interest in being, apparently, the first Mauritian species to be reported from South Africa.

A notable feature of this essentially shallow shelf fauna is that of the fifty-one species reported before from this region, twenty-nine have not been recorded from anywhere else. If at least a similar proportion of the forty-four new species described prove to be limited to eastern South Africa, then the endemic component of this fauna will be considerable. Millard (1978) showed that the endemic component of the South African hydroid fauna achieves its highest levels in the region between Cape Agulhas and Durban, and that while the eastern and southern regions of the South African shelf have a hydroid fauna with a substantial proportion of Indo-West-Pacific species, the character of the southern fauna, centred on Agulhas Bank seems sufficiently distinctive to confirm Briggs's (1974) contention that a separate faunal province may be recognized in this region. Bryozoan species diversity is frequently related to the availability of substratum and might be expected to be high on the Agulhas Bank. The most southerly of the stations represented in the present collections (SM 184, SM 185) were located at the northern extremity of the Bank; by analogy with Millard's (1978) results it seems probable that the South African bryozoan fauna may prove to be even richer than the present report suggests, and even more distinctive than the hydroid fauna.

The most exciting aspect of the geographical distribution patterns of the South African bryozoan fauna is the increasing evidence of strong similarities with eastern Australian and northern New Zealand faunas, and indications that this link may be of considerable antiquity. Three examples are given in Table 4: *Bugulella australis* and *Schizoretepora tessellata* have been reported elsewhere only from South Australia; *Escharina waiparaensis* was originally described from Miocene (Brown 1952) and Pliocene (Brown 1954) deposits of New Zealand, and subsequently live specimens were reported (Powell 1967) from Three Kings Islands, northern New Zealand. The occurrence of this species in South African waters is thus of the greatest interest. The new species described here also include several with equally extraordinary time–space distributions. For example, *Dimorphocella moderna* appears to be the only Recent representative of a genus well known from Australian Tertiary deposits. The large live colony was collected from the same station that produced the abundant, also live, material of *Aspidostoma livida*. Few Recent species of *Aspidostoma* are known, and most of these are small encrusting forms with a habit quite unlike the massive foliose colonies of *A. livida*. However, *Aspidostoma* also seems to be an ancient genus; Brown (1952) described a number of species with erect colony forms from New Zealand Tertiary deposits, and other fossil species are known from Australia (Maplestone 1902, 1911). *Macropora* is another interesting case; the genus is widespread through the Tertiary deposits of Australia and New Zealand, and one species with a long fossil history survives today in New Zealand and has also been reported from the Philippines. Few nominal Recent forms have been described; these

require re-examination and it is possible that *M. africana* may be only the second Recent form of this ancient genus.

A number of authors have published valuable integrated studies of Tertiary to Recent bryozoan faunas (for example, Lagaaij & Cook 1973; Cook & Lagaaij 1976; David & Pouyet 1978) that demonstrate the importance of such research to bryozoan phylogeny and the contribution it may make to the broader field of marine zoogeography. Bryozoans are particularly useful subjects for zoogeographical research; with very short larval lifespans, and consequent poor dispersal ability, with high species diversity in most shelf seas, and in many Tertiary deposits, and with perhaps rapid rates of phylogenetic change through time, they offer great potential for detailed analysis. As Lagaaij & Cook (1973) reiterate, wide distributions observed in Recent seas are the legacy of past expansions and contractions. The evident richness of the eastern South African fauna and its apparently high level of endemism, the numerous systematic affinities with the fauna of the south-west Pacific (see, for example, p. 47), and the number of ancient genera and species found in the present collections demand further investigation. Whether these features of the South African fauna reflect relict elements, or are truly autochthonous, can only be decided by further study of Recent populations, in comparison with Tertiary fossil deposits and Quaternary sediments.

SUMMARY

A total of 130 species of Bryozoa have been identified from samples collected by the R.V. *Meiring Naude* between 1977 and 1979. The sampling stations ranged in depth from 80 m to 900 m, with the majority in depths of less than 100 m. Bryozoan diversity was highest in the samples from the shallowest stations; 44 new species are described, including a high proportion of encrusting cheilostomata. The fauna described is considered to be representative of a typical shallow shelf-sea assemblage, in marked contrast to the deeper slope fauna reported upon in the first publication on the *Meiring Naude* Bryozoa (Hayward & Cook 1979). Together with the earlier contributions on the South African Bryozoa, referred to in the text, these two reports now provide a sound introduction to the bryozoan fauna of this region. Although some taxonomic problems remain and the question of broader systematic relationships is further complicated in some cases by these results, the particular character of the eastern South African fauna is more clearly defined and shown to include a substantial and distinctive endemic element. Further surveys on the Agulhas Bank may be expected to yield results that will further enhance this distinctiveness. Bryozoan skeletal remains were important components of biogenic carbonate sands in some of the areas sampled, and the presence of abraded fragments of unrecognized species in these sands shows that the taxonomic diversity of this fauna is still to be fully recorded.

The discovery of species and genera with extensive time–space distributions, and in particular the apparent faunal similarity between this region and Tertiary fossil deposits of Australia and New Zealand, suggest interesting and fruitful possibilities for further research.

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ABBREVIATIONS

Lz	length of zooid	lz	width of zooid
Lop	length of opesia	lop	width of opesia
Lor	length of orifice	lor	width of orifice
Lov	length of ovicell	lov	width of ovicell
Lg	length of gonozooid	lg	width of gonozooid
Loo.st.	length of ooeciostome	l br.z.	width of brooding zooid
L br.z.	length of brooding zooid	l br.or.	width of brooding orifice
L br.or.	length of brooding orifice	lm.	width of mandible
Lav	length of avicularium		
L ad.av.	length of adventitious avicularium		
L int.av.	length of interzooidal avicularium		
Lm	length of mandible		

BMNH British Museum (Natural History)
SAM South African Museum

APPENDIX 1

MEIRING NAUDE STATIONS THAT PRODUCED BRYOZOA

Station	Co-ordinates °S	°E	Depth, m	Date
SM 103	28°31,7′	32°34′	680	24.5.76
SM 123	30°33,4′	30°48,6′	690	10.5.77
SM 129	30°53,4′	30°31,7′	850	11.5.77
SM 131	30°43,2′	30°40,8′	780	11.5.77
SM 151	30°14′	31°27,6′	900	17.5.77
SM 162	32°55′	28°31′	630	25.5.78
SM 163	33°04,6′	28°06,6′	90	26.5.78
SM 164	33°04,6′	28°06,6′	90	26.5.78
SM 179	33°30,3′	27°22,1′	80	29.5.78
SM 180	33°29,4′	27°21,2′	80	29.5.78
SM 184	33°39,4′	27°11,7′	86	31.5.78
SM 185	33°39,3′	27°11,6′	90	31.5.78
SM 232	32°14,9′	29°10,4′	560–620	25.6.79
SM 233	32°15,2′	29°09,8′	540–580	25.6.79
SM 234	32°15′	29°09,1′	500–520	25.6.79
SM 239	32°14,8′	29°00,8′	90	25.6.79
SM 250	31°59,3′	29°22,5′	150–200	27.6.79

APPENDIX 2

INDEX TO GENERA AND SPECIES

Correct names are given in italic; synonyms in roman.

(atlantica, Idmidronea overleaf)

(Crisina overleaf)

(Holoporella capensis *overleaf*)

(Odontionella cyclops overleaf)

(stomachosum, Rhynchozoon overleaf)

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype
SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

P. J. HAYWARD
&
P. L. COOK

THE SOUTH AFRICAN MUSEUM'S *MEIRING NAUDE* CRUISES PART 13 BRYOZOA II

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ANNALS
OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

SEMPER ALIQUID NOVI AFRICA AFFERT

INSTRUCTIONS TO AUTHORS

1. MATERIAL should be original and not published elsewhere, in whole or in part.

2. LAYOUT should be as follows:

(a) *Centred masthead to consist of*
Title: informative but concise, without abbreviations and not including the names of new genera or species
Author's(s') name(s)
Address(es) of author(s) (institution where work was carried out)
Number of illustrations (figures, enumerated maps and tables, in this order)
(b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
(c) *Table of contents* giving hierarchy of headings and subheadings
(d) *Introduction*
(e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
(f) *Summary*, if paper is lengthy
(g) *Acknowledgements*
(h) *References*
(i) *Abbreviations*, where these are numerous

3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

Footnotes should be avoided unless they are short and essential.

Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

4. ILLUSTRATIONS should be reducible to a size not exceeding 12 × 18 cm (19 cm including legend); the reduction or enlargement required should be indicated; originals larger than 35 × 47 cm should not be submitted; photographs should be rectangular in shape and final size. A metric scale should appear with all illustrations, otherwise magnification or reduction should be given in the legend; if the latter, then the final reduction or enlargement should be taken into consideration.

All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters.

The number of the figure should be lightly marked in pencil on the back of each illustration.

5. REFERENCES cited in text and synonymies should all be included in the list at the end of the paper, using the Harvard System (*ibid., idem, loc. cit., op. cit.* are not acceptable):

(a) Author's name and year of publication given in text, e.g.:

'Smith (1969) describes . . .'
'Smith (1969: 36, fig. 16) describes . . .'
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(b) Full references at the end of the paper, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc. to the year for more than one paper by the same author in that year, e.g. Smith (1969*a*, 1969*b*) and not Smith (1969, 1969*a*).

For books give title in italics, edition, volume number, place of publication, publisher.
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Examples (note capitalization and punctuation)

BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.
FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
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(continued inside back cover)

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THE OUTLINE OF AN EIGHTEENTH-CENTURY ECONOMIC SYSTEM IN SOUTH-EAST AFRICA

By

MARTIN HALL

&

KATHLEEN MACK

Cape Town Kaapstad

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Natal Museum, Pietermaritzburg

(With 11 figures and 8 tables)

[*MS accepted 7 October 1982*]

ABSTRACT

In this paper different sorts of evidence are brought together in order to outline the economic system of a set of chiefdoms in south-eastern Africa in the late eighteenth century. Locations of capitals, given in recorded oral traditions, allow boundaries of chiefdoms to be modelled with a standard analytical technique. Faunal collections from archaeological sites indicate the economic role of livestock, and the carrying capacities of the chiefdoms are estimated from ecological data. Comparison of ceramic assemblages and architectural styles allows an evaluation to be made of the different roles of men and women in the larger economic structure.

CONTENTS

INTRODUCTION

For the people of south-eastern Africa the early years of the nineteenth century were a period of rapid change. During the preceding half-century many of the small chiefdoms between the Thukela and Phongolo rivers had come to owe allegiance to particular rulers either in a loosely structured confederacy, such as the Mthethwa under Dingiswayo, or in a more rigidly controlled system, such as the Ndwandwe state under Zwide (Marks 1967). In 1816, Shaka kaSenzangakhona succeeded to the Zulu chiefship and then came to control the Mthethwa confederacy. Defeating the Ndwandwe, he built a powerful military kingdom, which dominated south-eastern Africa for a further 60 years (Guy 1979).

Ann. S. Afr. Mus. **91** (2), 1983: 163–194, 11 figs, 8 tables.

Although it has been argued that the Zulu kingdom was in structure similar to the chiefdoms that it replaced (Hedges 1978), the formation of the kingdom involved a fundamental change in scale. For example, the regiments, or *amabutho*, were adapted from loose age-sets into highly organized military units incorporating the majority of the male population of fighting age (Wright 1978). This strengthening of the regiments involved a change in settlement pattern as large military towns were built at appropriate points around the kingdom. Similarly, the domestic economy, which was formerly centred on the homestead, had to be adjusted substantially to provide for the concentrated centres of population around the barracks. On a national scale Shaka was able to control a far wider political field than his predecessors, trading extensively and using his military power over a substantial sphere of influence (Guy 1979).

It is difficult to understand the way in which these various components of the Zulu kingdom were brought together as a cohesive political and economic system without understanding the crucial role of cattle—a point made eloquently and forcibly by Guy (1970, 1977). It was not just that cattle were important for their milk, their meat, and for secondary products such as hide. Cattle were also the medium through which women, important for their own labour power and for the labour power of the children that they would produce, were distributed among households. Thus the *lobolo* system of bridewealth, functioning within the patrilineal and patrilocal marriage system, allowed the head of an *umuzi* (homestead, pl. *imizi*) to acquire wives for his sons with payments from his herd. This herd could be replenished by *lobolo* received on the marriage of daughters, but also by patronage received from higher levels in the political hierarchy: local lineage heads, chiefs, and ultimately, the King (Bryant 1949, Guy 1979). Thus one of the more important functions of the Zulu military institution was to obtain cattle from areas beyond the kingdom by raiding, providing the King with a means of economic control.

Although agriculture was an important element in the economy, the welfare and reproductive potential of the Zulu cattle herds were of central importance. It is fair to deduce that access to suitable grazing areas was a factor in the struggle between the minor chiefdoms, and then between the Mthethwa and the Ndwandwe, in the years before Shaka's consolidation of the kingdom. This point was made perceptively by Daniel (1973), when he pointed out that those chiefdoms to emerge with power at the end of the eighteenth century appeared to control the most productive combinations of grazing types. Without falling prey to environmental determinism, it is fair to argue that any full understanding of the origin of the Zulu kingdom must be preceded by an appreciation of the economic geography of the area between the Thukela and Phongolo rivers.

In this paper a study is made of the cattle-based economy of kwaButhelezi and its immediate neighbours—one small group of chiefdoms in the years immediately before the formation of the Zulu kingdom. The aim is to try to discover more about the nature of cattle husbandry and the redistribution of

livestock by looking at faunal collections from archaeological sites, at ceramic typologies, and at the distribution of grazing resources within the boundaries of this particular group of chiefdoms. The results have only the status of tentative hypotheses, but they demonstrate that some pattern can be obtained from the diverse and fragmentary data available.

KWABUTHELEZI AND NEIGHBOURING CHIEFDOMS: ESTABLISHING BOUNDARIES

As a prelude to examining the pre-Shakan economy of kwaButhelezi, it is necessary to establish the extent of the landscape controlled by this chiefdom and by its immediate neighbours. The approach was to find the location of the principal seat of each chief in the closing years of the nineteenth century—the most important *umuzi* in each chiefdom, which for convenience has been termed the capital. Using these capitals as nodal points, the landscape has been divided through the use of Thiessen Polygons. This simple technique establishes the most rational use of an area (Haggett 1965) and has been used with some success in archaeological situations as diverse as Mesoamerica (Hammond 1972) and Iron Age hill-forts in southern Britain (Cunliffe 1971), as well as in an earlier study in a region immediately adjacent to kwaButhelezi (Hall 1981). It must be emphasized that the lines of the polygons that result from this technique need not be taken as definite territorial boundaries. There is evidence to suggest that chiefdoms in southern Africa were not normally defined in such a way, but were rather core areas of influence separated by ill-defined zones that were either not utilized or served as commonage (Ford 1971). Thus, although the Thiessen Polygons are here presented as firm lines, they can be taken as marking the positions of broad zones separating areas of political and economic control.

Although the *imizi* of south-east African chiefs were places of considerable importance, there is today often little physical evidence of their locations. Construction materials were usually wood, thatch, and clay and little has survived even of the larger centres such as Dingane's Mgungundlovu or Cetshwayo's Ondini. Archaeological traces, and in particular midden deposits, are found frequently, but at this level of physical decay it is difficult to tell royal settlements from ordinary Late Iron Age sites. In this situation the most profitable approach is to search for pointers in oral traditions. Unfortunately, many such traditions were lost during the formative years of the Zulu kingdom, when a large proportion of the smaller chiefdoms were destroyed and their populations relocated, thus breaking the lines by which histories had been passed through the generations. Despite this, enough information survives to piece together the outlines of the political geography of the pre-Shakan period.

A primary source is A. T. Bryant's *Olden times in Zululand and Natal* (1929). Although this author's florid style, with its classical allusions, ornate analogies and quotations from English poetry, serves as a heavy disguise,

Bryant's text does include a mass of invaluable historical information, which has been the subject of close study. The technique in extracting locational information from this text was first to study Bryant's map of 'Native clans as located in pre-Shakan times', which is reproduced at the end of his text, and to note the positions of chiefdoms in the area of concern. Textual references have been traced to areas controlled by the chiefs and to their residences in the late eighteenth and early nineteenth centuries. In most cases the location of the principal *umuzi* is given by reference to prominent hills or to rivers and it has often been possible to locate these places on standard 1 : 50000 scale maps.

A further important source of information has been the corpus of oral tradition collected by J. B. Wright of the University of Natal, Pietermaritzburg, on two visits to the Babanango area in 1975 and 1976. These data were collected systematically using the methods now standard among historians of African societies. Transcripts of these interviews are stored with the Department of Ethnoarchaeology, Natal Museum, Pietermaritzburg.

The locations of kwaButhelezi and neighbouring 'clans', as given by Bryant in his map, are shown in Figure 1. It is apparent from the text of Bryant's work, however, that not all clans had the same political status. Some were independent chiefdoms, governed by a single chief and exercising claim to a particular area. Others were subject to more powerful chiefs, exercising local control but with no ultimate sovereignty.

Although it is sometimes not possible to be conclusive, Bryant's references to the fortunes of the different chiefs and their houses provide a good indication of political status. Of the 'clans' shown in Figure 1, it would seem that kwaKhumalo, kwaZungu, and kwaMpungose were independent chiefdoms allied with no other houses. It is also clear that the Ncubeni were subject to the Buthelezi chief (Bryant 1929: 114) and that the Dludla formed part of kwaXulu (Bryant 1929: 229). Bryant (1929: 28) states that the Dlamini became subject to the Mbatheni chief late in the eighteenth century and that the Magwaza were a sub-clan of the Langeni house, which was formed early in the nineteenth century, after the period presently under consideration (Bryant 1929: 127). The Mazuku are given as an offshoot of the Qungebeni and, as their chief does not seem to have had independent political power, they have been considered a part of emaQungebeni (Bryant 1929: 687). Within kwaZulu have been included the Ntombela, a sub-clan of the royal house (Bryant 1929: 32), and the Sibiya, who had interacted politically and economically with the Zulu chiefs for many generations (Bryant 1929: 27). (It is difficult to find a neutral term for the lands of the Zulu chiefdom. The general 'Zululand', preferred by Guy (1979), is too imprecise in the present context, and so the locative has been used, as with other chiefdoms. This usage does not imply a connection with the present-day 'homeland' of the same name.) Finally, although the Magubane 'clan' is shown on Bryant's map, no mention is made of this group in the text. As it would thus seem unlikely that the Magubane were an independent chiefdom, they were probably subject to either the Khumalo or to the Buthelezi. For the purposes of

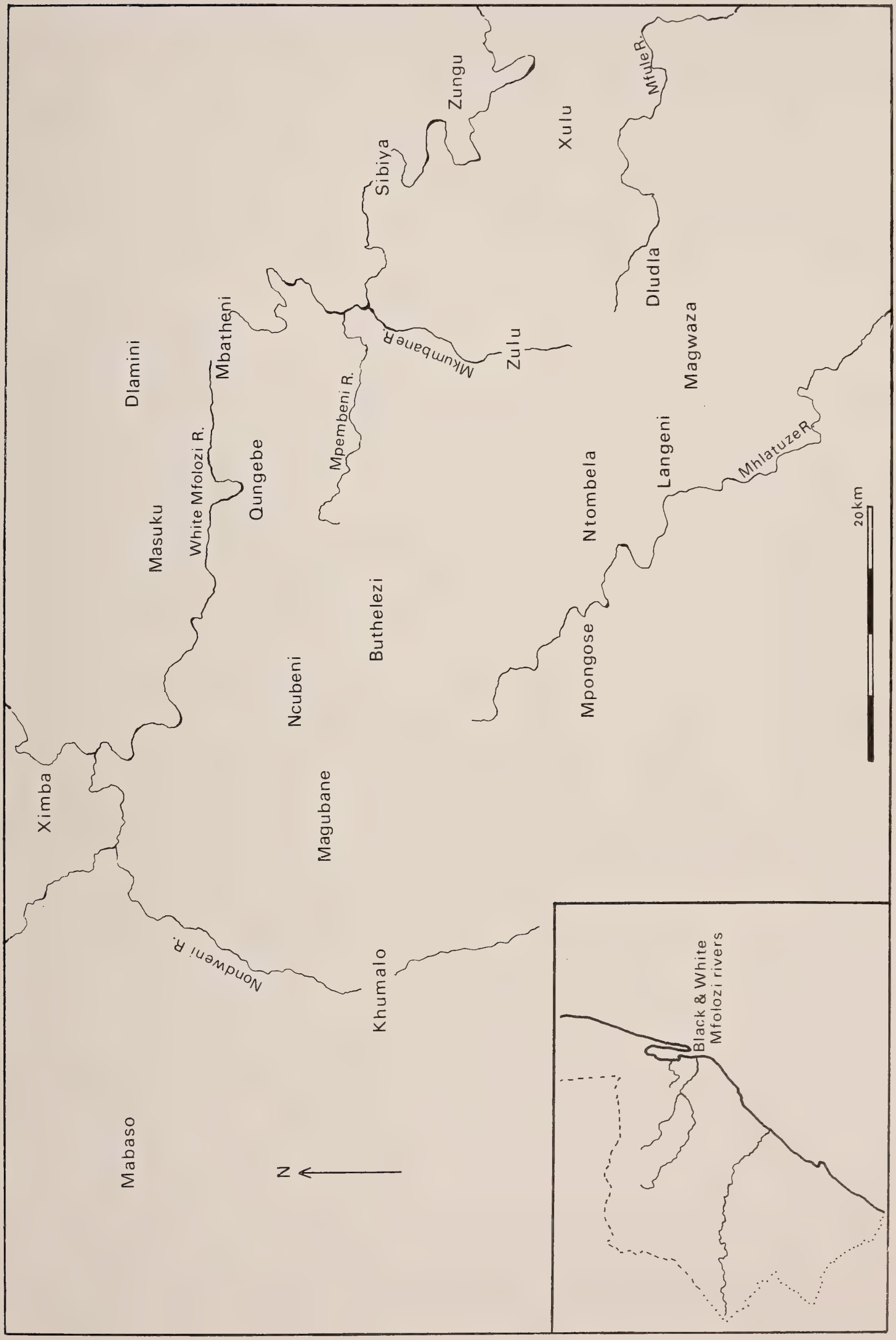

Fig. 1. 'Pre-Shakan Clans' of the study area, as mapped by Bryant (1929). Bryant's original spelling has been retained.

Fig. 2. Late eighteenth-century chiefdoms in the study area.

the following analysis they have been disregarded. A revised version of Bryant's map, showing the approximate locations of these chiefdoms and with the orthography corrected in accordance with modern practice, is shown as Figure 2.

According to Bryant (1929: 28), the founders of the Buthelezi royal house settled 'along the emCakweni ridge above the sources of the amaPopoma river and on to the Zulu borders'. At the end of the eighteenth century they were bounded by kwaZulu, emaQungebeni, and Babanango Mountain, although the chiefdom was still centred on the emCakweni Ridge (Bryant 1929: 131). The Buthelezi chief in the closing years of the eighteenth century was Phungashe, but Bryant provides no precise indication of the location of his capital. Oral traditions collected by Wright (1975), however, indicated four *imizi* successively occupied by Phungashe and a tentative sequence in which they served as capital of kwaButhelezi: eLangeni, the first of Phungashe's capitals (not to be confused with the chiefdom of the same name), oDwini, eMbamba, and, as Phungashe's last seat, emaGundaneni. Each of these sites was examined and all showed signs of occupation—a few potsherds and some broken grindstones. All the sites are within an area of a few square kilometres and, for the purposes of this analysis, eLangeni has been taken as the political and economic centre of late eighteenth-century kwaButhelezi.

Bordering kwaButhelezi to the south-east was the chiefdom of kwaZulu, ruled by Senzangakhona, father of Shaka. Surprisingly, but perhaps because the emphasis has been on describing the lands of the kingdom that was to come a few decades later, there is comparatively little information about the area under Senzangakhona's control. KwaZulu in the closing years of the eighteenth century was certainly centred on the valley of the Mkhumbane River, above its confluence with the White Mfolozi River but beneath the high lands of the Babanango Plateau. Bryant (1929: 20) describes the Zulu chiefdom as lying 'within a shallow hill-flanked valley, eight miles across'. The location of Senzangakhona's capital is, however, more definite. Bryant (1929: 46) attributes at least three *imizi* to Senzangakhona, although he states that the chief's principal wife was resident at only one of these, esiKlebheni. James Stuart's informant Baleni, however, referred only to esiKlebheni (Webb & Wright 1976: 41), as does Lugg (1949: 112), who states that this *umuzi* was built by Senzangakhona 'on attaining manhood' and that 'here he lived and died'. Bryant (1929: 46) records that esiKlebheni was located 'on the summit of a high rounded ridge . . . overlooking the right bank of the middle Mkumbane . . .'. Senzangakhona's grave, marked by a cairn, is on the site of his capital of which extensive midden deposits survive.

Further to the south-east were the chiefdoms of kwaXulu and eLangeni. Bryant (1929: 228) records that, in the decades before Shaka's rise to pre-eminence, the Xulu 'occupied the country between the Mfule and White Mfolozi rivers, on the seaward side of the Mtonjaneni heights'. Their chief was Xabashe and his capital, which is not named, was 'by the eLumbi hill, on the

left bank of the upper Mfule River' (Bryant 1929: 101). Xabashe's Langeni contemporary was Mbenge, who was a close relative of Nandi, mother of Shaka. Mbenge's capital was iNguga, which Bryant (1929: 48) locates 'by the isiZiba stream below emTinemide (near modern Melmoth)' and which Lugg (1949: 126) places on the farm Bull Run. According to Bryant (1929: 125), eLangeni incorporated 'the hill-country about emTinemide, overlooking the middle Mhlatuze river, on its northern side'.

To the north and north-east of kwaButhelezi, in and about the immediate valley of the White Mfolozi River, were emaMbatheni, emaQungebeni, and kwaZungu. The first of these chiefdoms was mostly to the north of the White Mfolozi, 'from the Sihlalo–Mabedlane line to that of the Ntlazatshe–Mfolozi', although by the end of the eighteenth century the Mbatheni had also settled on the southern banks of the Mfolozi (Bryant 1929: 223). The Mbatheni chief at the time of Phungashe was Khali, and his capital was beneath the Nhlazatshe Mountain to which the population would retreat when threatened (Bryant 1929: 225). EmaQungebeni was further down the White Mfolozi River, in the area of its confluence with the Mpembeni River. The Qungebeni chief in the closing years of the eighteenth century and in the early years of the nineteenth was Ntusi, and his capital was at the Ntuzuma Hill (Bryant 1929: 26, 130). Further down-river was kwaZungu, which extended towards the Ondini Plain and was centred on Chief Manzini's capial kwaMpungabi, close the kwaHlophekhulu Hill (Bryant 1929: 176–177).

South-west of kwaButhelezi was kwaMpungose. Bryant tells little of this chiefdom, except that it was 'towards the eTaleni hill' (Bryant 1929: 29). The names and location of the Mpungose chief and capital at the end of the eighteenth century are not known, but for the purposes of this analysis it has been assumed that the chiefdom was ruled from an *umuzi* close to eThaleni.

Finally, the chiefdom to the west of kwaButhelezi was kwaKhumalo. The Khumalo house split in the late eighteenth century, with the senior section remaining 'inland of the Babanango Hill, and thence away over the Nondweni River', and the junior branch moving away to the north (Bryant 1929: 419). The chief of the senior Khumalo house, which is of concern here, was, in the late eighteenth century, Magugu, whom Bryant (1929: 420) states was succeeded by Nkonyeni, Mtezuka, and Mzungeni. James Stuart's informant Mabhonsa stated that 'the amaKumalo of Mtezuka and Mzungeni lived about Zungeni mountain and on further east. They also lived on the land subsequently built on by Sirayo ka Xongo'. Sihayo kaXongo lived in the Nquthu area (Webb & Wright 1979: 24, 39). Additional information on the Khumalo distribution comes from oral traditions collected during fieldwork at the site of Nqabeni (Hall & Maggs 1979), when it was stated that the upper catchment of the Ntinini River fell within the area occupied by the Khumalo under Mzungeni.

The literature does not contain information on the location of the capital of this southern branch of the Khumalo during Phungashe's time. During

fieldwork at Nqabeni, however, the present authors were told that a site in the upper valley of the Ntinini River had once been occupied by the chief Mzilikazi. This information is unlikely to be accurate, as Mzilikazi was a chief in the junior Khumalo house and lived to the north. Nevertheless, it is possible that the Ntinini Valley site was once the seat of a Khumalo chief, but of different name; an interpretation that is supported by the nature of the site in question, which is marked by extensive stone ruins and is a particularly large example of a Type B settlement as defined by Hall & Maggs (1979). For the purposes of this locational study, the Ntinini site has been taken as the capital of kwaKhumalo.

The locations of the capitals of this group of chiefdoms provide the basis for the set of Thiessen Polygons shown in Figure 3. This map reveals a coincidence between the courses of the two principal rivers that run through the area, the White Mfolozi and the Mhlathuze, and the boundaries of the chiefdoms, a correspondence between projected territories and features of the landscape that has emerged in other studies in which the Thiessen Polygon technique has been applied (e.g. Cunliffe 1971), and one that suggests that the locations of the capitals are essentially correct and the method of analysis sound.

It is possible to test further the distributional model shown in Figure 3 by seeing to what extent the boundaries deduced through the use of Thiessen Polygons fall close to the natural features given as border markers in the oral traditions. The place names mentioned earlier that have proved possible to trace are shown in Figure 4, from which it can be seen that the coincidence with the pattern of Thiessen Polygons is generally good. Thus the emCakweni Ridge falls within kwaButhelezi and close to Phungashe's capital. Other border markers are the Mhlathuze River, Babanango Mountain, and Mpunga and Ntuzuma hills, and it can be seen from Figure 4 that these do, indeed, fall on, or a little beyond, the suggested perimeters of the chiefdom.

As mentioned earlier, few references to the borders of kwaZulu at the end of the eighteenth century have been found. Figure 4 does show, however, that the lower reaches of the Mkhumbane River fall within the territory demarcated with the help of Thiessen Polygons. Similarly, the boundaries of both kwaXulu and eLangeni, as given by Bryant, are in accord with the distribution of chiefdoms suggested by the locations of the capitals.

In the cases of emaQungebeni, kwaZungu, and kwaMpungose there is too little information preserved in the oral traditions to test the distribution patterns, and the boundaries shown in Figure 3 must, for the time being, be accepted uncritically. In the case of emaMbatheni, however, there is some conflict between Bryant's description of Chief Khali's realm and the boundaries projected with Thiessen Polygons. As Figure 4 shows, the territory demarcated by the White Mfolozi River and by the Sihlalo, Mabedlana, and Nhlazatshe mountains covers only the eastern part of the area predicted by the Thiessen Polygon method, and overlaps into emaQungebeni. Nevertheless, there is some

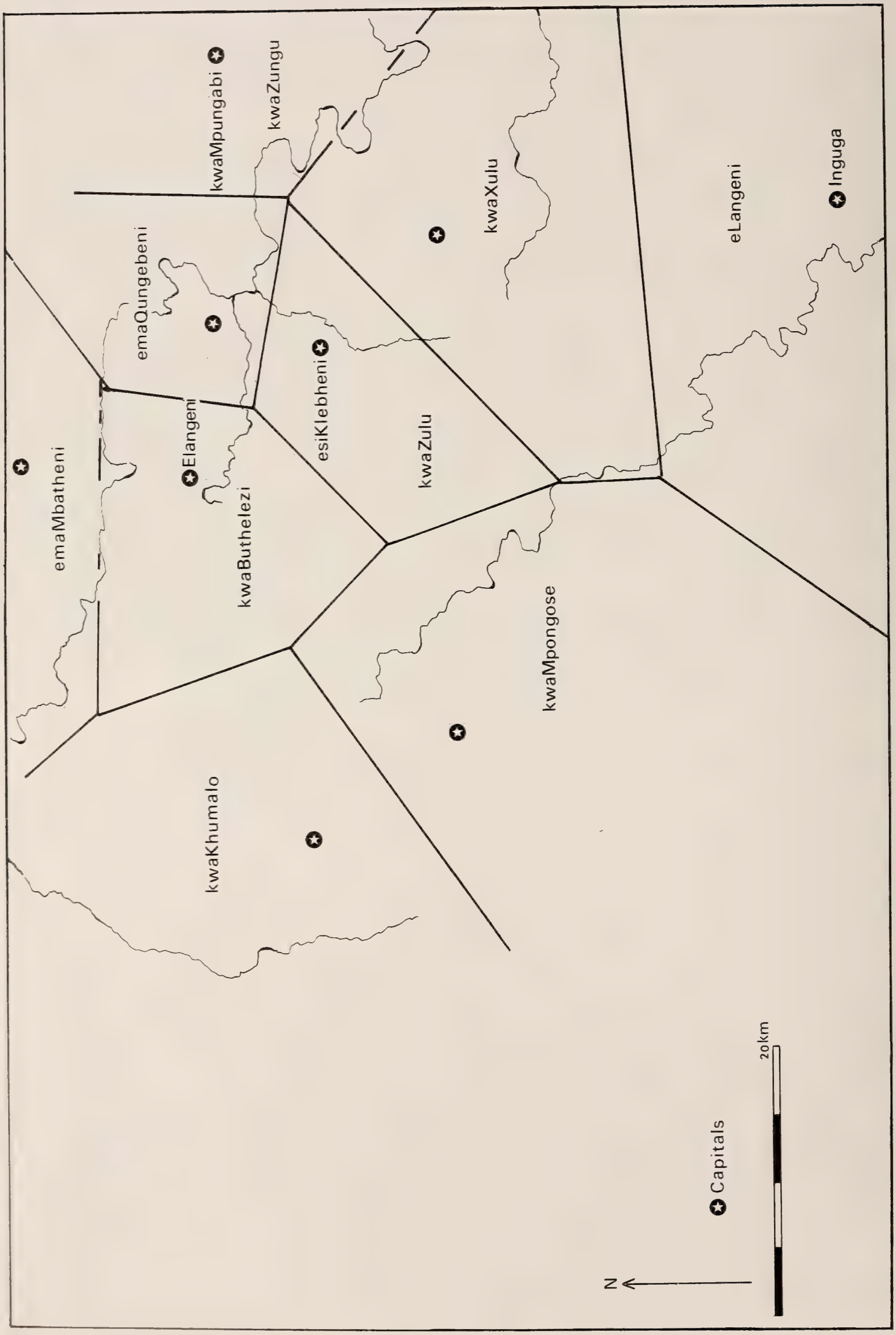

Fig. 3. Capitals of chiefdoms and boundaries projected with the Thiessen Polygon method.

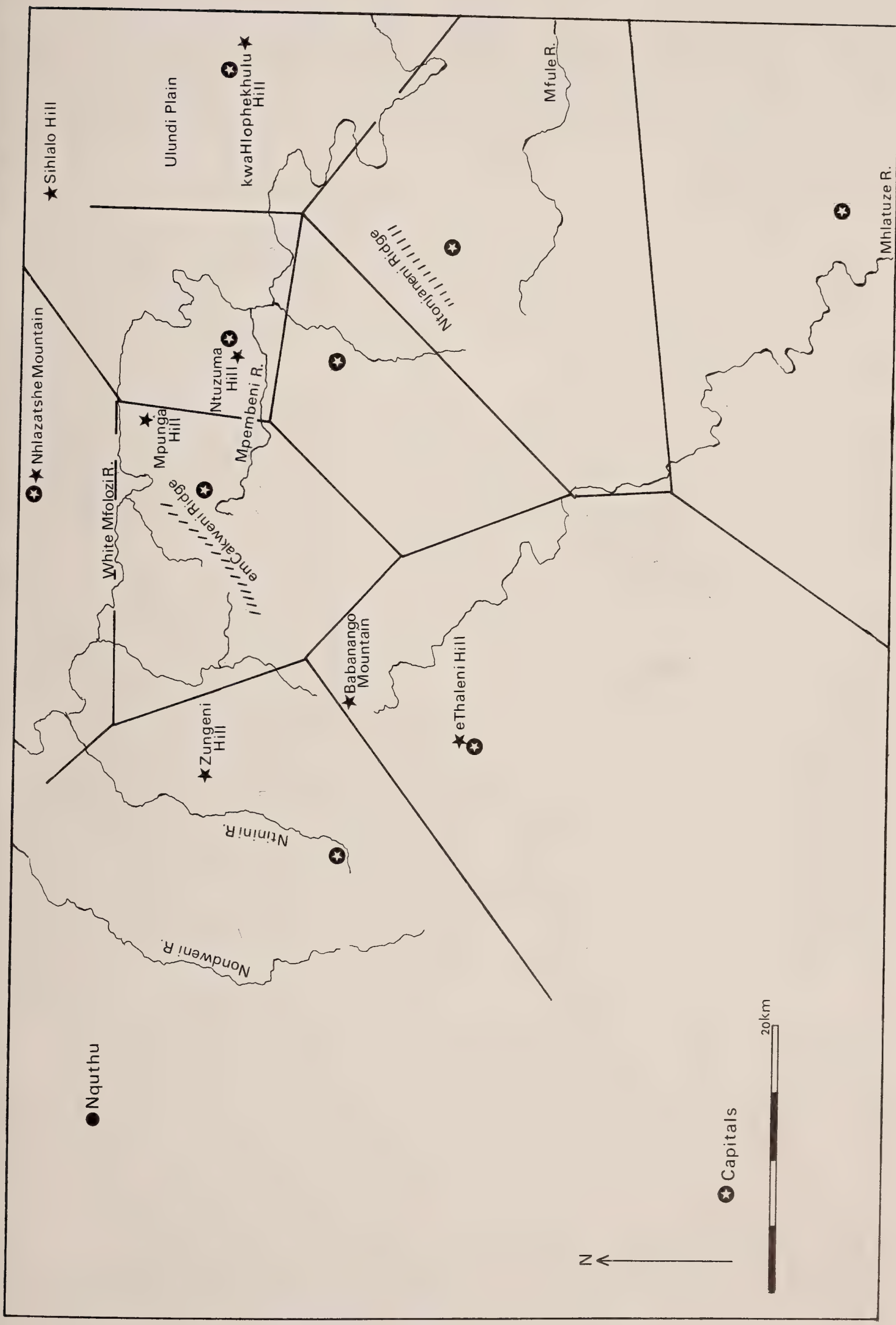

Fig. 4. Capitals, Thiessen Polygon boundaries, and boundary markers from oral traditions.

reason for preferring the area demarcated by the Thiessen Polygons. Bryant gives the location of Chief Khali's capital as Nhlazatshe and it would seem unlikely that the centre of the chief's power would lie on the very edge of the chiefdom. In addition, the border shown in Figure 3 coincides with the course of the White Mfolozi River, which would have formed a natural boundary line.

For kwaKhumalo, the fit between the oral evidence and the boundaries shown in Figure 3 is good. Bryant's description of the Khumalo as inland of Babanango Mountain is consistent with the opinion of James Stuart's informant, because Nquthu is to the north-west of the Nondweni River and Zungeni Hill lies on a line between this town and Babanango Mountain (Figure 4). In addition, the Ntinini River runs through the area encompassed by the Thiessen Polygon.

The method is thus shown to have produced a reasonable map of the chiefdoms in the White Mfolozi–upper Mhlathuze area during the decades that preceded the formation of the Zulu kingdom. Before using this map to examine the use of natural resources by the different chiefdoms, however, the evidence from archaeological excavation must be examined.

ARCHAEOLOGICAL EXCAVATIONS AT ELANGENI

As already mentioned, the site of eLangeni was pointed out by two informants, Hluphuyise Buthelezi, who is closely related to the Buthelezi ruling house and who was born late in the nineteenth century, and Mahlungwana Gabela, a younger man who is related indirectly to the Buthelezi chief Phungashe (Wright 1975). It was suggested that eLangeni was the first in a series of four *imizi*, all close to one another, that were used by Phungashe (Fig. 5), and it must be presumed from the approximately known dates of Phungashe's chiefship that eLangeni was occupied in the closing years of the eighteenth century. All four sites showed evidence of habitation, but eLangeni was chosen for excavation because it had apparently the best preserved midden deposits, thus promising information on the economy of Phungashe's capital, and because the site did not appear to have been much disturbed by ploughing.

The site is located on the gently sloping crest of a north-east facing spur, beneath a spring that, according to the informants, had produced water for the exclusive use of the Buthelezi chief. They were not able to identify any surviving remnant of the actual *umuzi*, but inspection showed isolated patches of ashy deposit and occasional potsherds in the shallow erosion cutting of a farm road and at one other point on the upper, south-westerly part of the site. Although farmers in the area told of shallow depressions that were visible after the grass on the site had been burnt and could have been the positions of dwellings within the *umuzi*, it was not possible to find any regular features of this nature on the site. Consequently, when it came to laying out the area for excavation, it was decided to concentrate on the patch of midden deposit at the

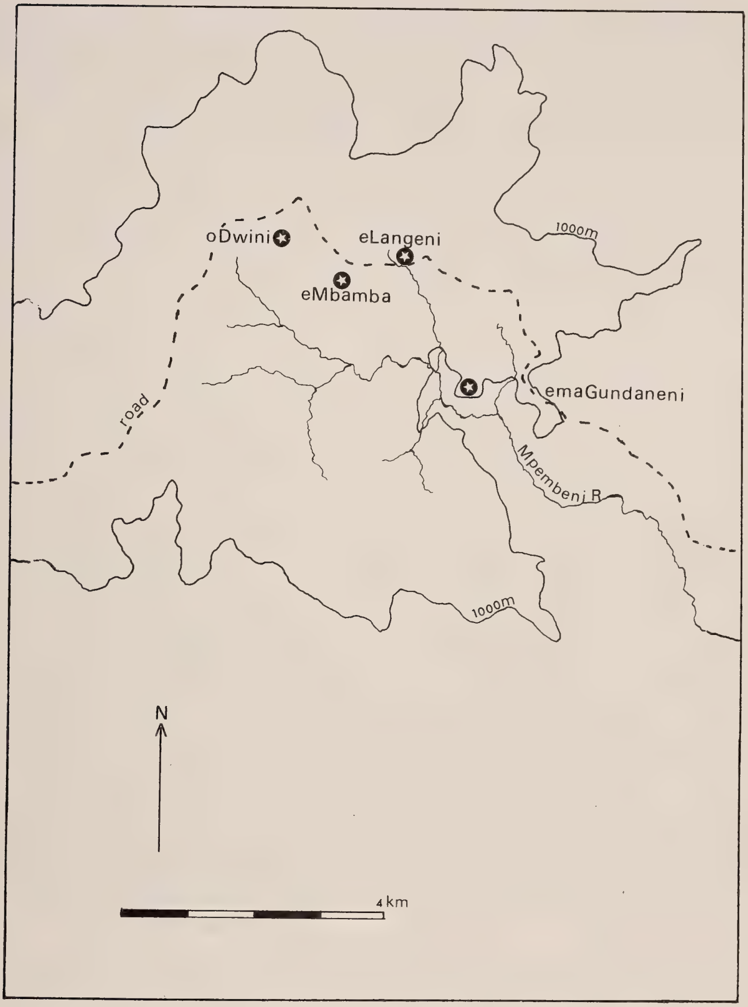

Fig. 5. Locations of Phungashe's four capitals.

upper end of the site. This decision was made for two principal reasons. Firstly, this midden area seemed to be better preserved than the exposures in the side of the farm road. Secondly, experience at Mgungundlovu, capital of the Zulu king Dingane several decades after Phungashe's chiefship located some twenty kilometres to the south-east, had taught that middens at the upper end of a royal *umuzi*, where the chief and his entourage would most likely have lived, tend to be archaeologically richer.

For excavation the midden deposits were gridded and the turf removed from one 10 × 8 m quadrant. It was apparent from the condition of the exposed deposit that there had been some disturbance by ant-bear (*Orycteropus afer*),

leading to the conclusion that the stratigraphy of the midden would prove to be disturbed considerably. In consequence it was decided to excavate in blocks of 8 m^2 and in 15 cm spits; a strategy further justified by the probability that eLangeni represents a single occupation.

As the aim was to recover a large sample of fauna and artefacts within the comparatively short time available for excavation, it was necessary to employ a recovery technique that would enable the midden deposits to be processed at a rapid rate but without an unacceptable loss of information. The solution was to use two mesh sizes: a coarse sieve of 25 mm^2 and a finer mesh of 6,5 mm^2. The use of the wider mesh allowed rapid processing of deposit, while the results of sieving with the finer mesh allowed biases to be identified and corrected when the results of the excavation were analysed. During the course of the excavation a tally was kept of the number of buckets of deposit that were removed from the excavation and processed through the coarse and fine sieve units respectively. The average volume and weight of the bucket-loads were calculated and these figures used to convert the bucket tallies into approximations of the volume and weight of deposits analysed.

The north and west sections through the eLangeni midden deposits are shown in Figure 6. Most of the midden consisted of a brown soil high in clay content but incorporating concentrations of ash and charcoal. This composition is reflected clearly in the stratigraphy, although the sections also demonstrate a degree of disturbance by animals. The topography at the base of the midden was investigated carefully, but there was no evidence of the type of structure found by Maggs (1982) at Mgoduyanuka.

Although the midden was excavated in regular units, it was decided to treat the faunal and artefactual collections from eLangeni as a single component. As has been noted, the evidence suggests that the site was occupied by a single group of people and for a period considerably less than the span of a single generation. It is therefore likely that the different lenses and slight

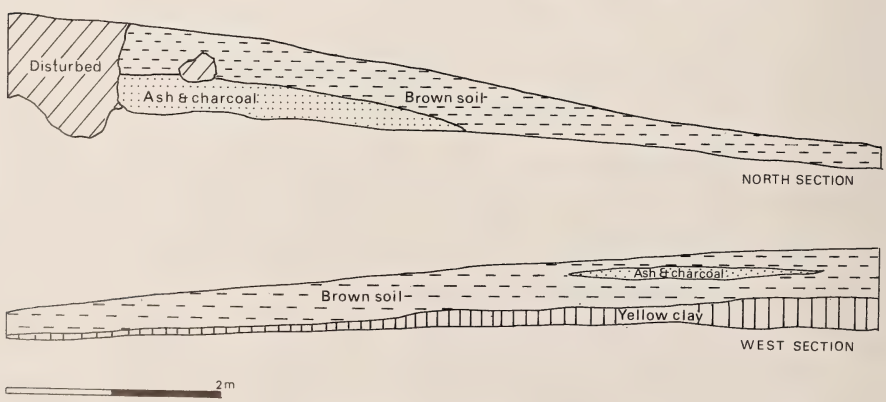

Fig. 6. Sections through the eLangeni midden.

changes in deposit colour that were apparent in the course of excavation were the result of different domestic activities, such as the cleaning out of fireplaces or damaged dwellings, rather than the product of different and separate occupations of the site. A further practical consideration was the degree of disturbance within the midden, which would have made a fine level of stratigraphic division superficial. No attempt was made to test assumptions regarding the date and span of occupation with radiocarbon determinations. Although carbon samples were collected in the course of excavation, the problems of calibration in the later phases of the Iron Age make the derivation of an independent radiocarbon chronology for sites such as eLangeni extremely difficult.

Approximately, 55,5 m^3 of deposit were removed from the eLangeni midden and passed through the sieve units. Of this total, 49 per cent was passed through the finer mesh and 51 per cent through the coarser sieve. As no classes of small artefacts, such as trade beads, were recovered from the midden, and as almost all the potsherds were sufficiently large to be retained by the larger mesh size, tests were carried out for systematic sample bias by examining the recovery record of the two sieve units for different size classes of animal bone. Table 1 shows the different proportions that nine classes of faunal specimens contributed to the assemblages from the coarse and fine sieve units and from both units combined. If the use of the larger, 25 mm^2 mesh for 51 per cent of the total sample had introduced a consistent loss of information, similar percentages should be expected of the categories of larger bone, such as bovid tooth rows and the identifiable bovid skeletal parts, and a smaller percentage figure for the coarse sieve unit for smaller categories of bone, such as bone flakes and miscellaneous skeletal parts. Table 1 shows that such a bias is not apparent in the eLangeni assemblage, where there are only slight differences between the percentages that make up the collections from the two sieve units.

TABLE 1

eLangeni: comparison of faunal recovery from coarse and fine sieve meshes.

Skeletal part	25 mm^2 mesh	%	6,5 mm^2 mesh	%	Total	%
Isolated bovid teeth	79	2,6	50	1,6	129	2,1
Bovid tooth rows	5	0,2	4	0,1	9	0,1
Bovid skeletal parts	183	6,1	162	5,1	345	5,6
Enamel fragments	23	0,8	38	1,2	61	1,0
Skull fragments	83	2,8	83	2,6	166	2,7
Vertebral fragments	91	3,0	69	2,2	160	2,6
Rib fragments	135	4,4	147	4,6	282	4,6
Bone flakes	634	21,1	584	18,3	1 218	19,7
Misc. skeletal parts	1 771	59,0	2 049	64,3	3 820	61,6
Total	3 004	100	3 186	100	6 190	100

Note. Specimens removed directly from excavations not included.

The test for sample bias included only the fauna recovered from the sieve units; other, generally larger and fragile, faunal remains were also collected directly from the excavation area. Table 2 shows the full faunal assemblage broken down into different categories. This analysis, as well as the identification of species and the estimates of age, was carried out by A. J. V. Brown with the facilities of the Department of Archaeozoology at the Transvaal Museum, Pretoria.

TABLE 2

eLangeni: total faunal sample.

Skeletal part	Number	% of total sample
Isolated bovid teeth	136	2,2
Bovid tooth rows	12	0,2
Bovid skeletal parts	437	6,9
Other identified remains	1	0,0
Enamel fragments	61	1,0
Skull fragments	166	2,6
Vertebral fragments	160	2,5
Rib fragments	282	4,5
Bone flakes	1 218	19,4
Misc. skeletal parts	3 819	60,7
Total	6 292	100

Minimum numbers of the different species that could be identified from the assemblage are shown in Table 3. It is clear that, with the exceptions of the lagomorph and the buffalo, which may have been hunted, the eLangeni assemblage consists of domesticated species of which 25 per cent are either sheep or goats and 68 per cent are cattle.

The tests for sample bias in the recovery technique employed for the eLangeni midden can also be taken as confirmation that the ceramic assem-

TABLE 3

eLangeni: minimum numbers of individuals identified from faunal sample.

Species	Subtotal		Total	% of sample
Ovis aries	2	Total *Ovis/Capra*	10	25
Capra hircus	1			
Ovis/Capra	7			
Bos taurus			28	68
Syncerus caffer	2	Total non-domesticates	3	7
Indet. lagomorph	1			
Total			41	100

blage is representative of the pottery used on the site. The composition of this assemblage is given in Table 4, from which it can be seen that more than 95 per cent consisted of undecorated and unburnished sherds, mostly from the bodies of vessels. The remaining small proportion of sherds do, however, have distinctive characteristics that allow an impression of the pottery industry from this site. The vessels that have been partially reconstructed are shown in Figure 7.

The vessels from eLangeni are simple in shape and comprise open-mouthed bowls (Fig. 7F–G), U-shaped or incurved bowls (Fig. 7A–D, K) and pots either without necks or with necks poorly defined (Fig. 7H–L). It has been possible to reconstruct thirteen vessels sufficiently to allow measurement.

TABLE 4
eLangeni: composition of the ceramic assemblage.

	Decorated sherds				Undecorated sherds				Totals
	matt	burnish	ochre	black	matt	burnish	ochre	black	
Rim sherds									
rounded	1	0	1	0	240	1	10	2	255
flattened	0	0	1	1	74	0	16	2	94
pointed	0	0	0	0	35	1	1	1	38
Body sherds	13	4	1	2	7 534	171	197	29	7 951
Total sherds	14	4	3	3	7 883	173	224	34	8 338

Of this small sample, two are open-mouthed bowls, with a mean maximum diameter, which is at the rim, of 12,8 cm. Nine U-shaped and incurved bowls, which are categories grading into one another, were measurable, and have a mean rim diameter of 13,1 cm and a mean maximum vessel diameter of 15 cm.

Only two pots could be reconstructed sufficiently for measurement. One of these (Fig. 7K) is a U-shaped vessel with a rim diameter of 10 cm and a maximum diameter of 12 cm. The other is a spherical pot with a rim diameter of 12 cm and a body curving out to a maximum diameter of 20 cm. An attempt had been made to drill a hole through this vessel, presumably to effect a repair. Although the other vessels in this category are too badly fragmented for measurement, it is clear that most of the pots from eLangeni are bag-shaped to spherical.

As mentioned, the majority of the vessels were undecorated and unburnished. It was noticeable, however, that when decoration and burnish did occur they occurred together. Decoration is simple, consisting either of impressions (as shown in Fig. 7P), or applied bosses, which are generally slightly elongated (Fig. 7M–O).

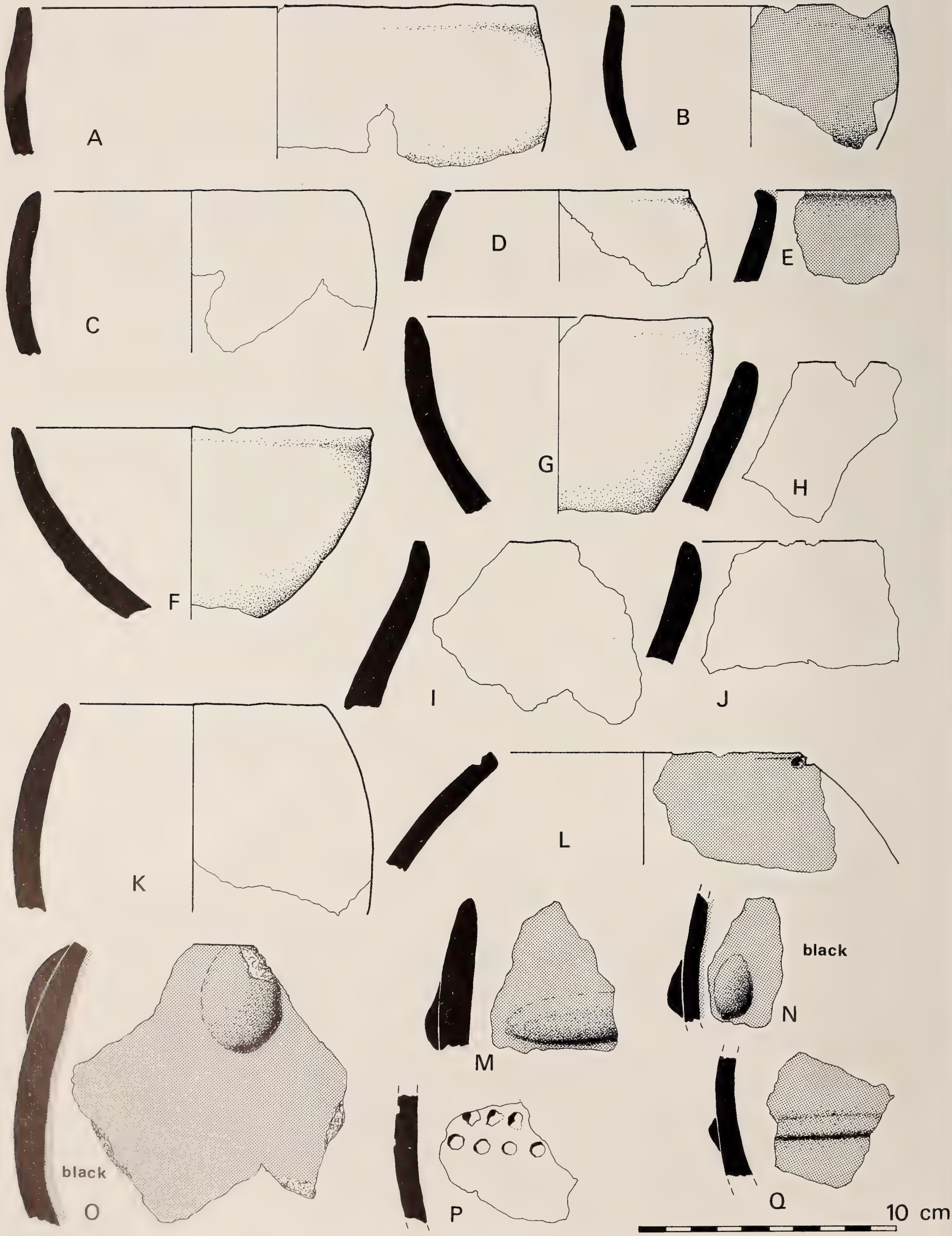

Fig. 7. The ceramic assemblage from eLangeni.

THE ECONOMIC SYSTEM OF KWABUTHELEZI

From the evidence for the boundaries of kwaButhelezi and neighbouring chiefdoms and the faunal and ceramic assemblages from the eLangeni excavations it is possible to outline the economic system of this region in the closing years of the eighteenth century and the first decades of the nineteenth century.

In the first place, additional information about the use of domestic cattle, which dominate the faunal assemblage from eLangeni, may be gained by establishing the ages at which the animals died. The results of this analysis, based on the study of dental eruption patterns, are shown in Table 5. It is clear from these data that cattle were kept until they were fully adult, as the majority of individuals died when they were older than 3½ years. This age profile of the eLangeni herd suggests that the emphasis was on rapid increase in herd size rather than on meat yield, for it is generally accepted that the ratio of carcass weight to fodder input is most favourable in sub-adult animals.

TABLE 5

eLangeni and Nqabeni: age of *Bos taurus* specimens on basis of tooth eruption.

	eLangeni		Nqabeni	
Age class	no.	%	no.	%
1. Less than 6 months	0	—	0	—
2. 6–15 months	1	4	2	6
3. 15–18 months	1	4	2	6
4. 18–24 months	3	11	2	6
5. 24–30 months	3	11	3	9
6. 30–42 months	3	11	4	12
7. Over 42 months	9	31	7	20
8. Breeding animals	6	21	8	23
9. Aged animals	2	7	6	18
Totals	28	100	34	100

In order to check that the eLangeni herd profile is a true reflection of general economic practice, A. J. V. Brown was requested to re-analyse the fauna from the contemporary site of Nqabeni, located in the neighbouring chiefdom of kwaKhumalo and originally described by Hall & Maggs (1979). The age structure of the Nqabeni herd is also given in Table 5 and the assemblages from the two sites are compared in Figure 8. It is immediately apparent that the herds kept in these two adjacent chiefdoms were very similar, and it seems justified to assume that this strategy of herd management was prevalent in this region during the period under discussion.

The observation that the eLangeni and Nqabeni herds were managed for maximum increment is consistent with the historical hypothesis, summarized earlier in this paper, that cattle were of key importance in the pre-Shakan

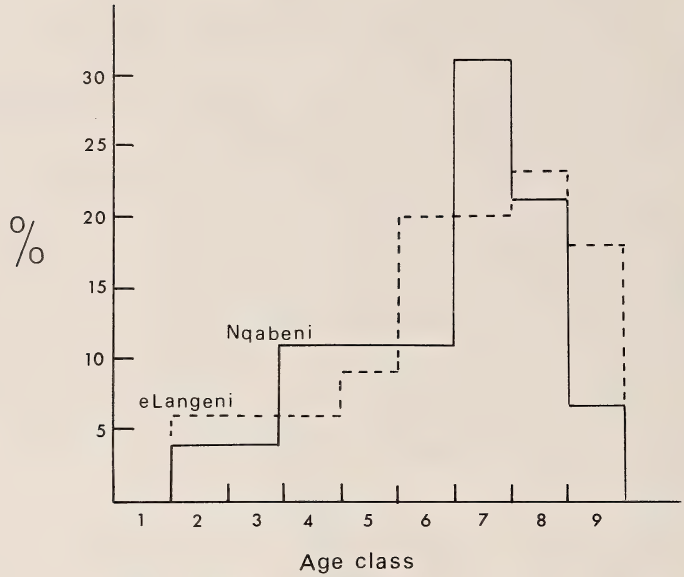

Fig. 8. Comparison of age profiles of cattle herds from eLangeni and Nqabeni.

economic system in this part of southern Africa. It is also logical to expect that access to suitable grazing and the quality of the sward were factors of concern to chiefs attempting to increase the size of their herds.

How can the characteristics of the different types of grazing available within the chiefdoms be assessed? A standard practice, reflected in, for example, the work of both Daniel (1973) and Guy (1979), has been to take the vegetation map published by Acocks (1953) as a model to distinguish between probable winter, summer, and intermediate grazing areas and to examine the dispersal of these economic resources in relation to the location of important chiefdoms and their capitals. Such a model has been useful at a general scale and has highlighted important correlations, but there are inadequacies in Acocks's map that make it less suitable for detailed analyses. The scale is such that important local variations are lost, while the map itself is based on the twentieth-century vegetation and does not take adequate account of the dramatic changes in flora that have been effected by $1\frac{1}{2}$ millennia of farming settlement (for a discussion of such changes see Hall 1981).

An alternative base for modelling pre-Shakan environments is Phillips's (1972) study of the ecology of the Thukela Basin and adjacent areas. Instead of working within a structure of vegetation types, which may vary with specific land-use practices, Phillips has combined information on landscape, soils, precipitation, and temperature and has delimited a number of 'bioclimatic regions'. This approach has the advantage of allowing the researcher to consider the possible states of different ecosystems under varying land-use

practices, rather than being bound by a classification drawn up from conditions at a specific time.

The major influence on the distribution of Phillips's bioclimatic regions is topography. The deeply incised river valleys, such as those of the White Mfolozi and the Mhlathuze, have produced bottomlands with low rainfall and rich soils. The interfluvial uplands, in contrast, have far more precipitation and soils which are often badly leached as a result of the percolation of nutrients following heavy summer storms. Because of these marked contrasts in structure, bioclimatic regions can be divided into three categories. Bioclimatic Region 4 (Phillips 1972: 107–119, 180–183), described as 'highland to submontane forest, short forest, thicket and short woodland/open woodland, humid to subhumid', forms a category by itself. These areas are now mostly an open, short grassland, although in the past there would have been more extensive forests and thickets. Thick sills of dolerite forming the interfluves between river systems often provide deep soils which, however, have often been leached by the heavy summer rains. As a result of this interplay between soil type and climate, grasses tend to shoot early in the summer growing season when they provide excellent grazing. Quality deteriorates during the summer months, however, and pasturage in the winter is very poor, necessitating very low densities of livestock.

In marked contrast is the environment of Bioclimatic Region 10 (Phillips 1972: 151–158, 195–198), described as 'subarid riverine and lowland mixed thicket and medium woodland/open woodland'. This region is confined largely to the river valleys where the winter dry season is pronounced and where there are frequently droughts during the summer months. Soils are from a wide variety of geological formations, as the river valleys have generally cut through the Karoo sedimentary series and into the Basement Complex. Low rainfall and gentle gradients have precluded leaching and soils have in consequence a high nutrient value, resulting in grazing that is palatable through the entire year. Severe moisture stress, however, makes such grasslands particularly vulnerable to overgrazing, and if productivity is not to fall they must be used lightly or rested when grasslands are available in other areas.

The intermediate group of bioclimatic regions consists of the valley slopes that lie between the upland plateaux and the valley bottoms. There is considerable variation in slope and aspect, but two clear sub-groups consisting of pairs of regions can be identified. Bioclimatic Regions 6 & 8 (Phillips 1972: 125–144, 184–193) can be considered together and are, respectively, the subhumid and mild subarid forms of the 'upland mixed thicket and short woodland/open woodland'. Soils are broadly similar, generally lying over Ecca formations and inherently poor in quality. Rainfall is lower than in the higher-lying Bioclimatic Region 4, and as a result grassland productivity is also low. In Bioclimatic Region 6, which is the better watered, early spring grasses are palatable for a while, but in Bioclimatic Region 8 even this early growth is of little value. In neither area is pasturage palatable in the dry winter months.

The second intermediate sub-category is made up of Bioclimatic Regions 2 and 3 (Phillips 1972: 83–106, 173–180). In contrast to regions 6 and 8, regions 2 and 3 tend to overlook the coastlands and therefore receive higher rainfall. This allows the greater development of woody vegetation, and some shells of the extensive forests of earlier years still stand. Again, soils tend to be leached and pasturage, where it exists, is of poor quality.

These bioclimatic regions can serve as a framework for calculating potential productivity for livestock when different land-use strategies are employed. In this part of the analysis, concern is restricted to these chiefdoms shown in Figure 3 that have a complete set of borders delimited by Thiessen Polygons —kwaButhelezi, kwaZulu, and (with the interpolation of a short stretch of the eastern border) kwaXulu. It will become clear, however, that the deduced land-use strategies of these three chiefdoms were probably also employed by other late eighteenth-century chiefs in the study area. The areas of the three different grazing types within each of the three chiefdoms are given in Table 6.

TABLE 6

Bioclimatic regions and total territory sizes for three chiefdoms.

Chiefdom	Region 4	Region 10	Intermediate	Total area
kwaButhelezi	94	66	167	327
kwaZulu	40	130	85	255
kwaXulu	44	226	300	570

Note. Figures are in km².

As a basis for estimating livestock productivity, use has been made of Mentis & Duke's (1976) study of the carrying capacities for wild herbivores of Phillips's different bioclimatic regions. Adjustments have been made where necessary, some of which are rough approximations, while others are based on informed assessments. Estimated carrying capacities over different grazing periods are given in Table 7. The unit of measurement is the Animal Unit (A.U.), which is defined as a mature domestic beast weighing 456 kg (Mentis & Duke 1976). Such a weight is probably considerably in excess of the size of a beast to be found in the eighteenth-century chiefdoms, but the A.U. is nevertheless a useful comparative measure.

TABLE 7

Carrying capacities of bioclimatic regions under different grazing periods.

Region	Summer only	Winter only	All year
4	67	N/A	20
Intermediate	33	N/A	N/A
10	N/A	28	14

Note. Figures are in Animal Units/km².

The estimate for the carrying capacity of Bioclimatic Region 4 with summer use only is taken directly from Mentis & Duke's figure of 1,5 ha per A.U. These authors assumed, however, that winter productivity in these high grasslands would be the same as in the summer months, an assumption that is clearly inappropriate in the present study. On the basis of comments by N. Tainton (University of Natal, 1979 pers. comm.) the more realistic estimate has been adopted that each Animal Unit will require 5 ha if kept in Bioclimatic Region 4 for the entire year.

It has been more difficult to arrive at a reasonable figure for the intermediate grazing types (Bioclimatic Regions 2, 3, 6, and 8). Mentis & Duke state that, at low density, wild herbivores can be kept on these grassland types all year, but Phillips's (1972) comments on grass quality in the winter months suggest that this would not apply to domestic stock if supplementary feeds were not available. Therefore the intermediate bioclimatic regions have been assumed to be unusable in winter and 3 ha have been allowed for each animal grazing in summer, a conservative estimate based on Mentis & Duke's figures for the same grazing period.

In the case of Bioclimatic Region 10, the valley areas, Mentis & Duke have been followed, allowing 7,2 ha per A.U. if the grasses are exploited throughout the year. For the situation in which stock are removed for 6 months the carrying capacity has simply been doubled.

There are three possible options that the chiefs of kwaButhelezi, kwaZulu, and kwaXulu could have employed in utilizing these grazing lands available for their cattle herds. First, livestock could have been kept in the same bioclimatic regions at comparatively low densities throughout the year. Secondly, the entire herd of each chiefdom could have been moved between winter and summer grazing areas in the form of the general transhumance often assumed for this sort of environment. Thirdly, chiefs and local headmen could have adopted a more flexible approach, moving some animals but leaving others in suitable grazing-areas throughout the year.

Taking into account the configuration of bioclimatic regions within each set of boundaries, it has been possible to calculate the different levels of productivity that could have been obtained by each chiefdom using each of the three options. The results are shown in Table 8. In calculating herd size with the first land-use option, in which livestock are not moved, the areas of Bioclimatic Regions 4 and 10 given in Table 6 have been converted by means of the carrying capacity estimates given in Table 7; note that as it has been assumed that livestock could not have been kept in the intermediate bioclimatic regions throughout the year, this first land-use option would not involve the utilization of Bioclimatic Regions 2, 3, 7 and 8.

If the entire herd of a chiefdom were to have been moved on a seasonal basis, the limiting factor for herd size would have been the lesser in carrying capacity of either Bioclimatic Region 10 or Bioclimatic Region 4 combined with the intermediate areas. For all three chiefdoms this constraint is, in fact,

TABLE 8

Projected herd sizes for chiefdoms using three different land-use strategies.

Chiefdom	Option 1	Option 2	Option 3
	(no transhumance)	(full transhumance)	(mixed strategy)
kwaButhelezi:			
Animal Units	2 804	1 848	3 728
land utilized	49%	29%	66%
kwaZulu:			
Animal Units	2 620	3 640	4 200
land utilized	67%	79%	100%
kwaXulu:			
Animal Units	3 964	6 328	7 208
land utilized	47%	65%	81%

imposed by available winter grazing lands in Bioclimatic Region 10. In each case, therefore, the livestock-carrying capacity with this second option can be derived by multiplying the area of Bioclimatic Region 10, given in Table 6, by the livestock density figure for the region if the grass is used for only 6 months of the year (Table 7).

Herd sizes given in Table 8 for the third option, when transhumance is combined with perennial grazing according to the specific availability of different environments within each chiefdom, have been calculated by first estimating the number of livestock that could have been carried when Bioclimatic Region 10 was used in the winter only, then checking that all the summer requirements of this itinerant herd could have been met with available intermediate bioclimatic regions (allocating a portion of Bioclimatic Region 4 for summer grazing if necessary), and finally by calculating the number of additional animals that could have been kept perennially on the remaining portion of Bioclimatic Region 4.

Table 8 allows these three strategies to be evaluated in two different ways. On the one hand, there are clear differences in the numbers of Animal Units that each strategy permits. Secondly, the percentage of the total territory of the chiefdom that each strategy utilizes gives some measure of the efficiency of each herding system.

In the case of kwaButhelezi, it is clear from Table 8 that the shortage of winter grazing would have made straightforward transhumance impracticable, allowing only a comparatively small-sized herd and utilizing only 29 per cent of the Buthelezi grazing lands. The first option of perennial pasturing would have been more productive, allowing a significant increase in herd size but still utilizing only 49 per cent of the chiefdom. Clearly the most productive land-use strategy would have been the third option, for this would have allowed a herd size more than double the size that could have been supported by mass transhumance alone, and would have involved the utilization of some 66 per cent of the land within kwaButhelezi.

Circumstances were clearly different in kwaZulu. This chiefdom had an adequate supply of winter grazing, with the result that large-scale transhumance would have been a far more attractive option. Nevertheless, Table 8 shows that a further increase in productivity could have been obtained by pasturing some animals in these parts of Bioclimatic Region 4 that were not required for the seasonal relief of the lowlands. It is apparent that the situation was similar in kwaXulu. Here again, large-scale transhumance would have been a logical management system, but some surplus upland grazing would have been available for the year-round maintenance of some additional stock.

How can it be established which, if any, of these three options was actually employed by each chiefdom? It is not reasonable to assume that in each case the land was used automatically to its fullest potential; other, unknown constraints may have been in play and there are many situations in which maximization cannot be assumed automatically (Hall 1981). One test is to examine site location in relation to the different grazing types, with the possibility in mind that the location of the chief's capital may reflect the predominant pattern of land-use within his chiefdom.

In Figure 9 the position of the capitals and the network of Thiessen Polygons have been superimposed on the map of bioclimatic regions. Immediately a strong correlation is apparent. Capitals are mostly located on or close to the boundaries of bioclimatic regions and in the more productive Bioclimatic Regions 4 and 10 rather than in the intermediate areas of grazing.

In addition, the positions of the capitals reflect the different optimal land-use strategies for each chiefdom. Thus the capital of kwaButhelezi is situated on the edge of Bioclimatic Region 4, reflecting the equal importance of this region, on which about half the Buthelezi herd could have been grazed perennially, and the combination of Bioclimatic Region 10 and the intermediate grazing areas, between which the remaining half of the livestock could have been moved with the seasons. The locations of the capitals of emaMbatheni, kwaMpungose and, perhaps, kwaKhumalo suggest that these chiefdoms might have managed their herds in similar manner. In the same way, the locations of the capitals of kwaZulu and kwaXulu reflect the overriding importance of a transhumance system in which winter grazing was crucial, a system probably also used in eLangeni, kwaZungu, and emaQungabeni (Fig. 9).

Thus this exercise in locational analysis and economic modelling suggests that the late eighteenth- and early nineteenth-century chiefdoms in this area adopted strategies that took best advantage of the possibilities of the environment. Although there is no theoretical basis for assuming maximization of cattle production, it does seem to have been applied in this case, a finding quite consistent with the faunal evidence from the sites of eLangeni and Nqabeni, indicating that a culling policy was adopted that would have allowed herd size to have been increased as rapidly as possible.

Further information about the economy of kwaButhelezi and neighbouring chiefdoms comes from settlement architecture and ceramic assemblages. In

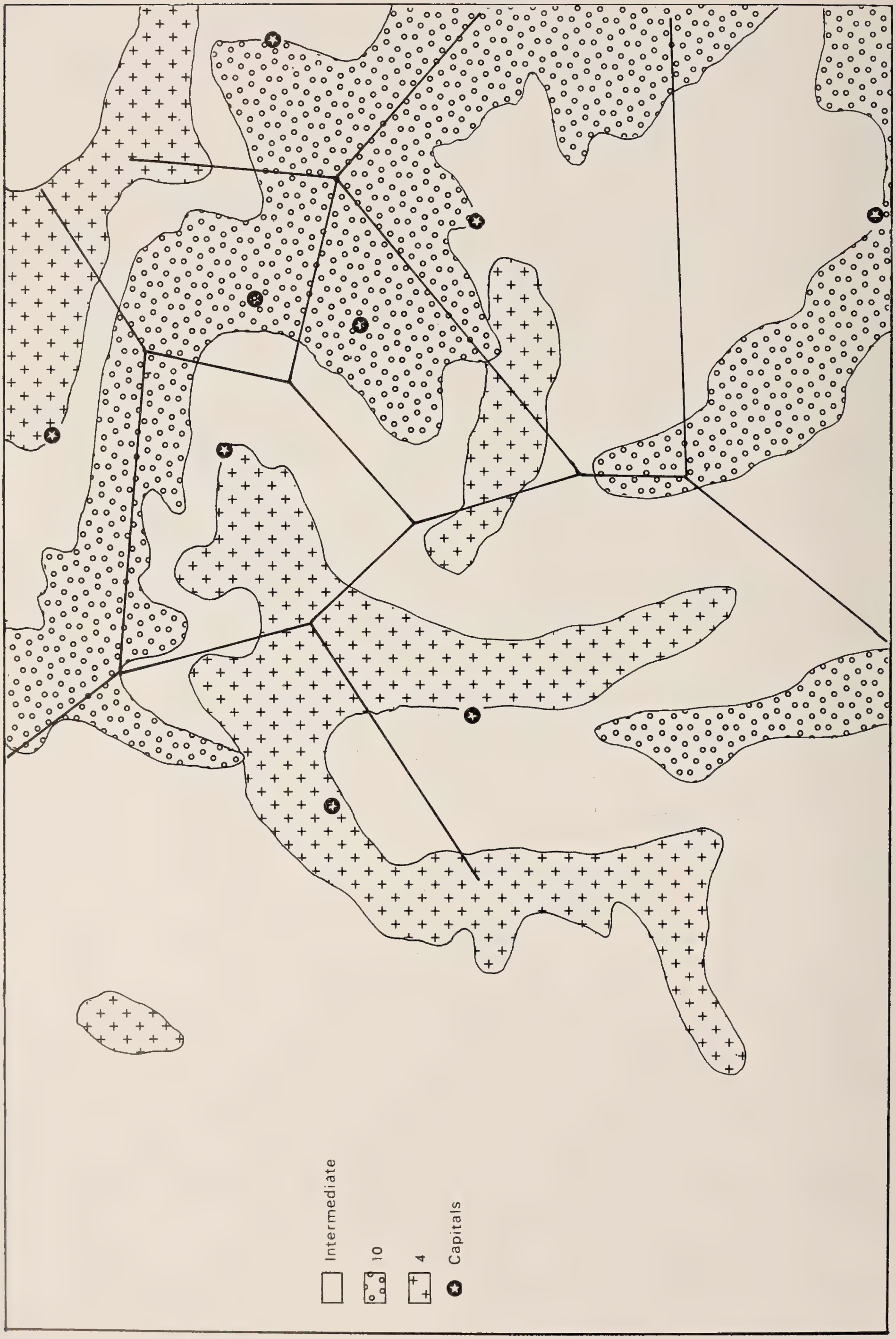

Fig. 9. Capitals, chiefdoms, and bioclimatic regions.

using these sources to infer elements of economic systems, two working assumptions are made: first, that pottery-making was predominantly a female activity with the design elements that provide the defining characteristics of a ceramic assemblage passing from mother to daughter or between women, and secondly, that the design of *imizi* was determined by men with architectural traditions passing from father to son or between men. These patterns of behaviour are deduced from the ethnographic literature, which indicates that women were responsible for cooking and brewing, the main activities involving pottery vessels, while the livestock herds, the requirements of which dictated the design of the village, were the preserve of the men (Bryant 1949; Krige 1965). Although such ethnographic parallels are dangerous, they are also a fruitful source of tentative models for interpreting the later prehistory of areas such as these.

Sites such as eLangeni and most of the capitals of neighbouring chiefdoms today contain no apparent evidence of their architecture. Clearly, structures were made from perishable materials—wood, grass and unfired clay. In the western part of the study area, however, the situation was different, for in these regions large parts of each *umuzi* were built with stone, with the result that information concerning settlement design is available today. A large area has been searched for these settlements and, as a result, it has been possible to classify sites by their design and to study the distributional properties of each settlement category (Hall 1981). Here the concern is with a group of sites known as Type B, which are distinctive, dispersed over a wide area, and were utilized during the late eighteenth and early nineteenth centuries (Hall 1981). Figure 10 shows the site of Nqabeni, a typical Type B site and the one from which the faunal assemblages described earlier in this paper were excavated (Hall & Maggs 1979).

An overall impression of the dispersal of Type B sites has been given in an earlier publication (Hall & Maggs 1979) and it is apparent, from comparison with Bryant's (1929) map, that there is a broad coincidence with the areas covered by kwaKhumalo and by kwaMabaso, a chiefdom that, in the years before the establishment of the Zulu kingdom, extended westwards beyond the Khumalo domain. What is of interest in the present context, however, is the strong correlation between the easternmost line of Type B sites and the boundaries between kwaButhelezi, kwaMpungose, and kwaKhumalo projected with the use of Thiessen Polygons (Fig. 11). This coincidence is unlikely to be the result of sample bias as much of the area falling within kwaButhelezi was searched intensively for stone-built settlements. Those recorded, however, were not of Type B.

There is no apparent ecological or functional explanation for the eastward limit of the Type B dispersal. Reference to Figure 9 will show that there is no coincidence with environment, as the occurrence of Type B sites falls off sharply within an expanse of Bioclimatic Region 4. Similarly, availability of raw materials for settlement construction is not likely to have been a factor.

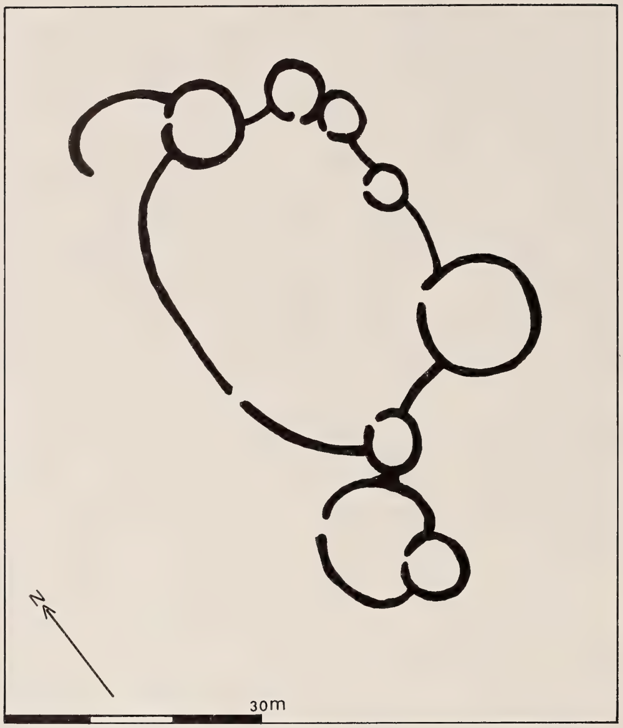

Fig. 10. Nqabeni, a typical Type B site in kwaKhumalo.

Although wood must have been available to build eLangeni and the other three Buthelezi capitals, this probably came from the wooded slopes of the Babanango Plateau where it falls away towards the White Mfolozi River in the eastern part of the chiefdom. The western part, in contrast, was probably treeless and similar to the lands of kwaKhumalo, a deduction that is supported by the occurrence of simple, single enclosures built of stone in western kwaButhelezi (Hall & Maggs 1979; Hall 1981).

It seems probable that Figure 11 reflects a 'cultural' boundary, that is to say, a distinction reflecting community identity rather than ecological or economic necessity. Thus in kwaKhumalo and, probably, in kwaMabaso men designed complex, multiple enclosures for their livestock, while in kwaButhelezi single enclosures were preferred, built of wood or, when this material was not available, of stone.

In contrast, pottery design was noticeably similar in the two chiefdoms. Comparison of the vessels from the Buthelezi site of eLangeni, illustrated in Figure 7, with the ceramics from Nqabeni (Hall & Maggs 1979) shows that the two assemblages are clearly part of a common tradition. Similar bag-shaped pots and spherical pots occur at both sites and the bowls are also much the

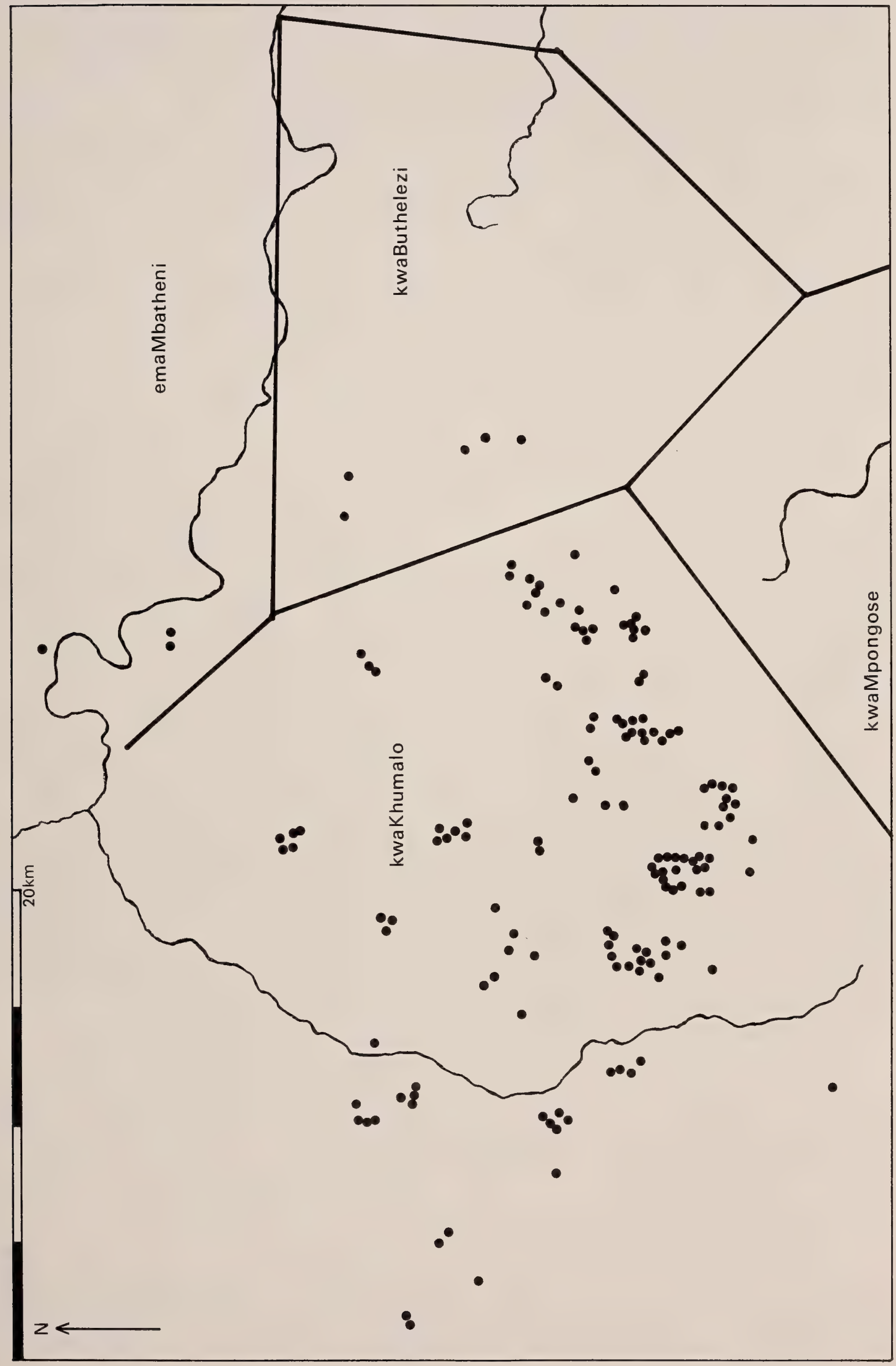

Fig. 11. The distribution of Type B sites and the boundaries of chiefdoms (site locations from Hall 1981).

same. On both sites the rarity and the form of decoration are definitive characteristics. Thus, although the ceramic evidence is less substantial than the testimony of architectural style, there is little sign that women were designing their domestic utensils differently in the two chiefdoms.

This patterning in the artefactual configurations of the study area is consistent with the economic model for the region which has been presented by historians and was summarized at the beginning of this paper. Thus the borders of the chiefdoms were politically important, incursions were contested by the chiefs, and the forms of male-dominated activities, such as settlement design, were passed down through lineages within the boundaries of chiefdoms. Women, in contrast, moved freely between chiefdoms as marriages were arranged across borders. The women took with them traditional concepts of pottery design, with the result that similar ceramic assemblages are found over a broad region. It can be assumed that livestock were also moved between chiefdoms as vital components in the marriage settlements.

A glimpse of this system in operation can be gained by taking Senzangakhona's matrimonial history as an example. The Zulu chief appears to have had about sixteen wives during his lifetime (Bryant 1929). Of the women whose parental origin is recorded, four appear to have been from other clans within kwaZulu. A further five brides, however, came from other chiefdoms: Nandi from eLangeni, Mpikase from emaQungebeni, okaSondaba from kwaButhelezi, Magulana from the Nqadini chiefdom, which was in the Mfule River Valley downstream from kwaXulu, and Ncaka from the Qwabe, a chiefdom in the valley of the Mhlathuze River. Despite this extensive marriage network, however, there was frequent friction between kwaZulu and neighbouring chiefdoms; indeed, Bryant records that Phungashe and Senzangakhona fought throughout their long reigns.

In conclusion, an overview can be offered of the economy of kwaButhelezi and neighbouring chiefdoms in the decades before Shaka absorbed such independent polities into the Zulu kingdom. KwaButhelezi would seem to have been an average-sized chiefdom, and Phungashe probably controlled an area similar in extent to neighbouring kwaZulu. Cattle were an important element in the economy, and there was an emphasis on increasing herd size rapidly, both in kwaButhelezi and in neighbouring chiefdoms such as kwaKhumalo.

KwaButhelezi had essentially an upland economy. Little winter grazing was available, and so it is logical to expect that about half the national herd were pastured permanently in the most favourable of the upland grazing areas. The remaining animals were probably moved between river valley and valley margins with the seasons. In contrast, neighbouring chiefdoms such as kwaZulu, where more winter grazing was available, moved the majority of animals on a regular basis.

There was a certain amount of ambiguity in the relations between neighbouring chiefdoms. Politically, there was often a state of conflict, with territorial differences promoting minor skirmishes. In this sphere, the boundaries

between chiefdoms were clear and they were further emphasized by artefactual distinctions such as the differing designs of settlements. Economically, however, there was frequent interaction. Chiefs took brides from the houses of neighbouring chiefs in marriage settlements involving the transfer of livestock. It may be presumed that similar transactions took place at lower levels in the lineages, albeit for smaller *lobolo* payments. Such free movement of women is reflected in the cosmopolitan nature of ceramic design, which reveals a tradition that did not respect the borders of chiefdoms.

Although the results of this study cannot indicate explicit reasons for the origin of the Zulu kingdom, it is felt that they do contribute to the understanding of the economic geography of this part of south-eastern Africa during a crucial phase of its history. It has been shown that diverse sources of evidence, such as faunal assemblages, oral traditions and ceramic collections, can be used within an appropriate methodological framework to provide illumination of historical problems.

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Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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Holotype
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Note standard form of writing South African Museum registration numbers and date.

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MARTIN HALL
&
KATHLEEN MACK

THE OUTLINE OF AN EIGHTEENTH-CENTURY ECONOMIC SYSTEM IN SOUTH-EAST AFRICA

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A REASSESSMENT OF THE RELATIONSHIPS OF PERMIAN DICYNODONTIA (REPTILIA, THERAPSIDA) AND A NEW CLASSIFICATION OF DICYNODONTS

By

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(With 40 figures)

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ABSTRACT

The type specimens of several genera of Permian dicynodonts have been re-examined and, where possible, prepared. Diagnoses of the following genera have been drawn up: *Eodicynodon*, *Endothiodon*, *Pristerodon*, *Tropidostoma*, *Rhachiocephalus*, *Oudenodon*, *Aulacephalodon*, *Pelanomodon*, *Dicynodon*, *Robertia*, *Diictodon*, *Emydops*, and *Kingoria*. Other genera have also been discussed.

Suites of derived characters have been formulated for each genus and used to draw up a cladogram of the phylogenetic relationships of the genera. A classification has been erected from the cladogram, using a methodology based on cladistic principles.

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INTRODUCTION

The Dicynodontia were a large group of herbivorous therapsids that probably arose during the Permian. By the end of the Permian they were the dominant herbivorous element of the fauna, but subsequently diminished in numbers with only a few representatives surviving into the Triassic. There is evidence that some forms were distributed world-wide.

The earliest forms generally recognized as belonging with the Dicynodontia (*sensu* Romer 1966) are from the *Tapinocephalus* Zone of the Beaufort Group of South Africa. These were small animals (skull length up to approximately 10 cm) that retained postcanine teeth but lacked incisors. By contrast the latest Triassic forms were large animals (skull length approximately 570 cm) that had lost all trace of teeth and had developed to the full the horny beak characteristic of the group.

In their skull characteristics dicynodonts constitute one of the most specialized of the therapsid groups. The preorbital region is short and in later forms the premaxilla and maxilla are edentulous, apart from the variably present pair of large canine tusks. In these forms a horny beak, similar to that of chelonians, is generally considered to have been present. The zygomatic arch flares laterally and is emarginated ventrally so that it becomes a narrow bar running posteriorly and dorsally in the skull. Posterior to the zygoma the squamosal flares laterally and is overlain anteriorly by the quadrate and quadratojugal. The lateral plate of the squamosal and the external surface of the zygoma provide attachment areas for jaw adductor musculature (the adductor externus lateralis), a situation unknown in therapsids outside the cynodonts. The quadrate forms a double condyle. The articular surface of the lower jaw is shallowly concave, then convex more posteriorly, and permits a sliding action on the quadrate. It is generally agreed (Watson 1948; Crompton & Hotton 1967; Cluver 1971) that such sliding would allow areas of the palate and the lower jaw to come into contact and triturate food matter. Protraction of the lower jaw would also allow the anterior tips of the upper and lower jaws to make contact and effect a 'beak-bite'.

In the palate the lateral pterygoid process is much reduced from the pelycosaur condition and directed anteriorly. A secondary palate formed by the posterior extension of the premaxilla and the medial extension of the palatines is present in later forms and is incipient in early representatives. Palatal teeth are lost.

The lower jaw does not have a coronoid bone. A mandibular fenestra between dentary and angular is present, and adductor muscles inserted on the outer surface of the jaw ramus as well as internally.

This character suite is used to define the Dicynodontia in the present paper. Any forms that fall within this definition will be referred to informally as dicynodonts, rather than dicynodontoids, dicynodontids, and so on.

Although there is a growing body of knowledge concerning the morphology and functional anatomy of dicynodonts, it has proved difficult to synthesize individual contributions since the taxonomy of the complete group has not been adequately worked out, despite the efforts of several workers (e.g. Toerien 1953; Cox 1959; Keyser 1975; Keyser & Cruickshank 1979; Cluver & Hotton 1981). Hammer & Cosgriff (1981) noted recently that 'the unresolved issues [touched upon here] are typical of the currently fluid state of dicynodont taxonomy and emphasize how little is understood about the natural groupings within this infraorder'.

There are various reasons for this state of affairs: the abundance of dicynodont material, the numerous taxa created on inadequately prepared and figured material, the loss of key type specimens, and the intractability of the matrix in which the earliest forms have been found. The present authors believe that any attempt at classification of dicynodonts should be based as far as possible on the re-examination of original type material, and that only type material that is reasonably well preserved and prepared should be considered. Forms that cannot be adequately diagnosed (especially incomplete or single specimens) should be left for the present *incertae sedis* until further preparation or additional specimens make their relationships clearer.

To this end type and other material in South Africa, the United States, and Great Britain was re-examined by either or both of the authors. Where possible, further preparation of the specimens was carried out. Since most of the described species and genera are of Upper Permian age and the taxonomy is most confused among these, it was decided to pay particular attention to the establishment of adequate diagnoses of these forms. The Triassic forms, in any case, have recently been reviewed by Keyser & Cruickshank (1979).

Furthermore, it was felt that diagnoses should as far as possible take into account derived characters, as opposed to shared primitive characters, so that relationships among genera could be established according to methods of Hennigian systematics.

The review has been confined to the generic level. The status of species within genera has not been discussed but it is recognized that this must be attempted at some future stage.

The genera reviewed and classified in this paper are: *Eodicynodon*, *Endothiodon*, *Pristerodon*, *Tropidostoma*, *Rhachiocephalus*, *Oudenodon*, *Aulacephalodon*, *Pelanomodon*, *Dicynodon*, *Robertia*, *Diictodon*, *Emydops*, *Myosaurus*, *Cistecephalus*, and *Kingoria*. All these genera, with the exception of *Eodicynodon* and *Myosaurus*, are from the Upper Permian of the Beaufort

Group of the South African Karoo Supergroup. *Eodicynodon* is from the upper Waterford Formation of the preceding Ecca Group (Rubidge & Oelofsen 1981), while *Myosaurus* is from the base of the Triassic of the Beaufort Group.

Assignment of localities to the various stratigraphic zones of the Beaufort Group follows the work of Kitching (1977), which in the opinion of the authors presents the most practical guide to Karoo biostratigraphy.

REDESCRIPTION AND DIAGNOSIS OF PERMIAN GENERA

Genus *Eodicynodon* Barry, 1974

Type species *Eodicynodon oosthuizeni* Barry, 1974

Type material

Skull lacking anterior part of snout and lower jaw, ROZ 1.

Locality

Zwartskraal, Prince Albert district, Cape Province.

Stratigraphic horizon

Upper Waterford Formation, Ecca Group (Rubidge & Oelofsen 1981).

Remarks on the type specimen

In a series of papers Barry (1972, 1974, 1975) described the stratigraphic occurrence, morphology, and systematic position of *Eodicynodon oosthuizeni*. Barry's 1974 paper contains a full description of the specimen. The most important features of the skull that set it apart from other dicynodonts are the paired vomers and premaxillae and the strong lateral processes of the pterygoids (Figs 1–2). These features represent the primitive therapsid condition as seen in pelycosaurs.

Description of additional specimens of Eodicynodon

Barry (1974) listed other specimens from the same locality as the holotype ROZ 1, and two of these specimens (ROZ 9 and 11) have since been prepared out of extremely hard matrix with the aid of dilute acetic acid to expose all bone completely. Details of these specimens complement what has already been described of *Eodicynodon* and, in view of the position of *Eodicynodon* as unquestionably the most primitive South African dicynodont known, it is felt warranted to describe the additional specimens in some detail. ROZ 9 is an incomplete skull with lower jaw and associated left forelimb and manus (Figs 3–6); ROZ 11 is an incomplete skull lacking lower jaw (Figs 7–8). The estimated original lengths of the two skulls are 80 mm (ROZ 9) and 70 mm (ROZ 11). The following description is based on both specimens.

A striking feature of the maxilla is a deep notch in the palatal rim in front of the well-developed tusk (Figs 5–6), so that in lateral view the rim is deeply

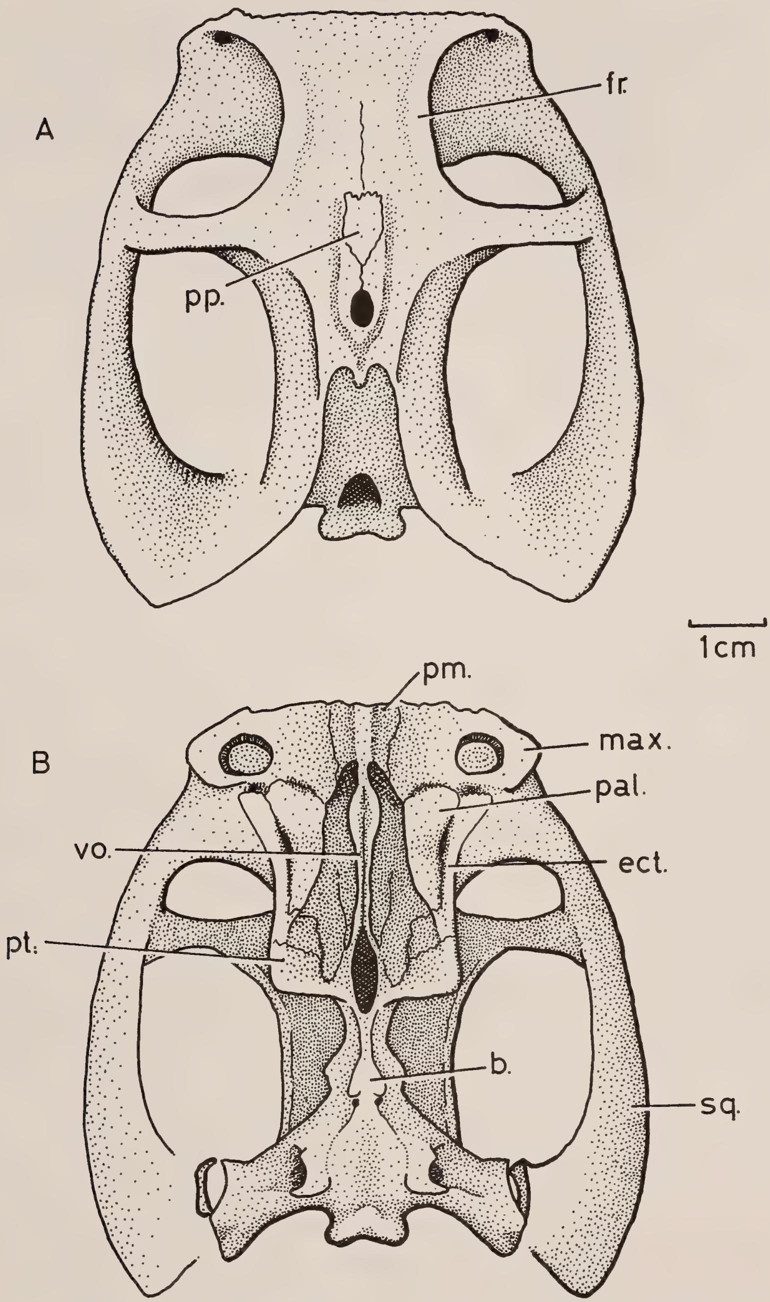

Fig. 1. *Eodicynodon oosthuizeni*. Type specimen ROZ 1, from Zwartskraal, Prince Albert. A. Dorsal view. B. Ventral view.

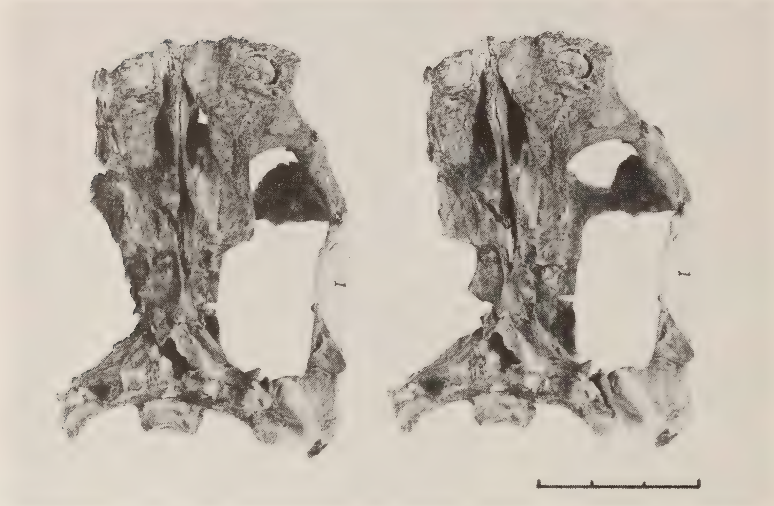

Fig. 2. *Eodicynodon oosthuizeni*. Type specimen ROZ 1. Stereophotograph of skull in ventral view. Scale in cm.

incised in a way not seen in other dicynodonts. In ROZ 9 an empty socket medial to the base of the right tusk, as well as what appears to be the base of a small, broken-off tooth in the corresponding position on the left side, indicate that teeth other than the tusks were present. In ROZ 11 there are two small teeth on the alveolar margin in line with the centre of the tusk. Two teeth are also present medial to the tusk. On the right side one small and one larger tooth are present, but on the left side only a single tooth can be made out. Small teeth are also present on the lower jaw of ROZ 9 (see below).

In the midline, where the premaxilla meets the vomerine interchoanal septum, a small portion of the premaxillary crest is preserved.

In the upper part of the incompletely preserved snout of ROZ 9 the floor of a fairly extensive maxillary antrum lies behind the root of the tusk. A narrow, slit-like opening leads through the anteroventral border of the orbit into the antrum on the left side; no counterpart of this opening can be seen on the right side of the skull.

The choanal opening in the palate differs from that of other dicynodonts in that a narrow, slit-like portion extends far forward to the level of the centre of the base of the tusk. Posteriorly the choana becomes shallow and wide between the pterygoids. The ventral edge of the vomerine septum is excavated as a deep trough widening posteriorly to merge with the interpterygoidal vacuity. In the roof of the trough a longitudinal suture indicates the meeting of the paired vomers.

The palatine has a swollen anteroventral palatal portion that does not project far medially into the choana. The ventral surface of this portion is rugose, contrasting sharply with the smoothly finished surrounding palatal

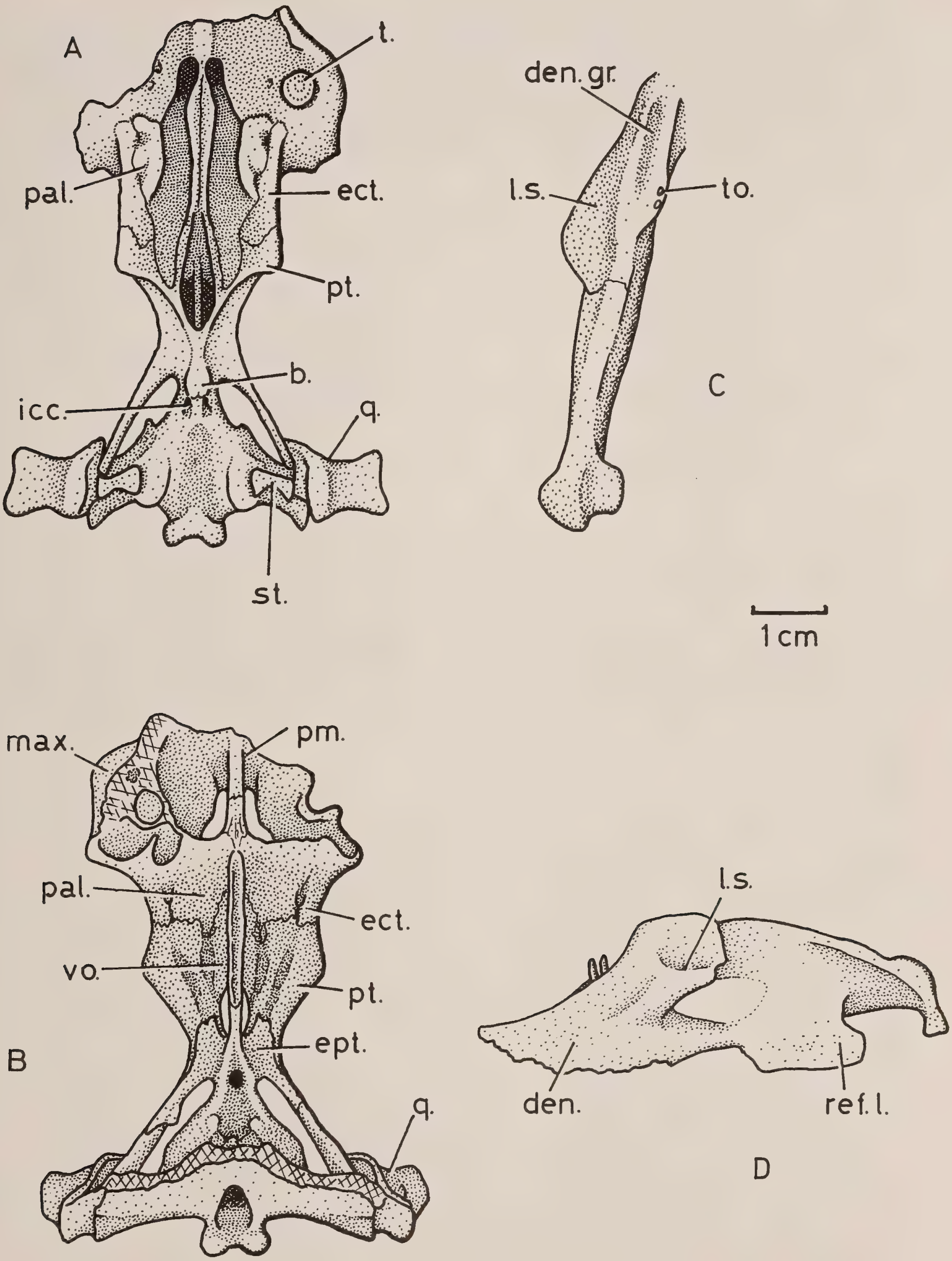

Fig. 3. *Eodicynodon oosthuizeni*. ROZ 9, from Zwartskraal, Prince Albert. A–B. Skull in ventral and dorsal views. C–D. Left ramus of lower jaw in dorsal and lateral views.

bones, and evidently carried a horny pad during life. Dorsally the palatine curves upward towards the midline to form a roof for the choanal passage, and posteriorly it terminates as a narrow wedge alongside the interpterygoidal vacuity. A lateral palatal foramen between the palatine and ectopterygoid opens dorsally on to the posterior surface of the jugal, continuing upward as a short groove.

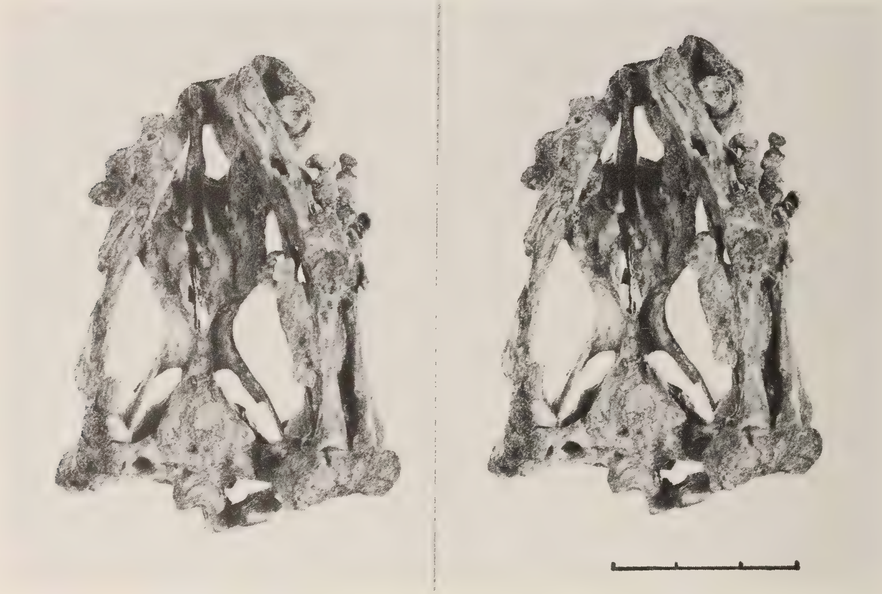

Fig. 4. *Eodicynodon oosthuizeni*. ROZ 9. Stereophotograph of skull and lower jaw in ventral view, with partial left forelimb. Note deep notch in palatal rim anterior to left maxillary tusk. Scale in cm.

Dominating the ventral view of the skull is a prominent ventrally directed pterygoid flange or process making up the ventrolateral border of the choanal space. The posterior corner of the process is also the most ventral part of the pterygoid and compares in position with the lateral pterygoid process of non-dicynodont therapsids.

Behind the interpterygoidal vacuity the pterygoids unite and together with the basisphenoid form a prominent ventral crest in the midline. Behind the contact with the basisphenoid each pterygoid extends posterolaterally as a quadrate ramus to terminate in a recess in the medial surface of the quadrate.

The epipterygoids are represented only by their footplates, but there are indications that these bones carried anterior and posterior cartilaginous extensions during life. Thus the dorsal surface of each pterygoid carried a groove leading forward from the front of the footplate of the epipterygoid up to the pterygoid-ectopterygoid suture, and it is likely that this served to house an anterior cartilaginous extension arising from the sharply truncated anterior

edge of the footplate. The posterior edge of the footplate, also truncated, suggests the former presence of a posterior cartilaginous footplate extension, which may have reached back to a recess in the medial surface of the quadrate above the posterior tip of the quadrate ramus. Such a posterior extension of the footplate in *Lystrosaurus* has been described (Cluver 1971).

The quadrate conforms to the standard dicynodont condition and from its relationships with the articular it is clear that the anterior-posterior sliding

Fig. 5. *Eodicynodon oosthuizeni*. ROZ 9. A. Stereophotograph showing detail of palatal area of skull. B. Stereophotograph of skull and lower jaw in dorsal view. Scales in cm.

motion between the two bones, characteristic of dicynodonts, was fully developed.

The stapes, well preserved on each side, lies in the usual position between the ventrolaterally facing fenestra ovalis and the inner surface of the quadrate. The bone is remarkable in that it is pierced by a large and nearly complete stapedial foramen, broken only where two thin dorsal processes of the stapes fail to meet. Among other dicynodonts a stapedial foramen is known only in *Cistecephalus* but it is present in pelycosaurs and in most other therapsid groups.

The interior of the braincase has been fully exposed and all the main features can be identified. As in other dicynodonts, the jugular foramen is large and the exoccipital is pierced by two hypoglossal nerve foramina. In the floor of the braincase the basioccipital carries a strong medial crest that rises anteriorly to terminate behind the hypophysial fossa. The sacculocochlear recess opens into the cranial cavity by means of a wide internal auditory meatus and above this the prootic carries a deep floccular fossa.

On each side of the shallow but distinct hypophysial fossa an ossified pila antotica rises some distance dorsally and anteriorly, while in front the floor of the fossa is pierced by the common internal carotid foramen. An anterior basicranial ossification, identified as the presphenoid in *Lystrosaurus* (Cluver 1971), lies clasped in the cultriform process of the parasphenoid in front of the carotid foramen. The anterior part of the cultriform process is an open, steep-sided trough, which evidently received the ventral edge of a cartilaginous interorbital septum in life.

As far as can be seen, the occipital plate conforms to the general dicynodont pattern. A portion of the squamosal is preserved on the right side of ROZ 11, overlapping the front of the occipital plate and closing off a laterally placed posttemporal fenestra. As in other dicynodonts, a channel from the anterior opening of the posttemporal fenestra leads up the lateral surface of the prootic and supraoccipital to a notch in the side of the braincase wall. This channel most probably housed a blood-vessel draining blood from the neck to the interior of the braincase before leaving the skull via the jugular vein (see Cox 1959; Cluver 1971).

Both halves of the lower jaw of ROZ 9 have been damaged and the symphysial region is entirely lacking. The following description is based on the more complete left half (Figs 3, 6). The dentary appears to have been a relatively massive bone with a clear lateral crest for attachment of the lateral division of the jaw adductor musculature (Crompton & Hotton 1967; Cluver 1975; King 1981). Behind the symphysial region the dorsal surface of the dentary carries a shallow groove, but posteriorly this surface is rounded and leads back to the raised dorsal boundary of the lateral dentary ledge. Behind the dorsal groove two slender teeth are situated on the inside edge of the dentary. The large mandibular fenestra is bounded by the dentary, surangular, and angular. Behind the fenestra a prominent reflected lamina of the angular extends far ventrally and is extended anteriorly and posteriorly along its ventral

Fig. 6. *Eodicynodon oosthuizeni*. ROZ 9. Stereophotograph of skull and lower jaw in lateral view, with partial forelimb and manus. Note deep notch in maxillary rim in front of tusk and distinct lateral shelf on dentary for adductor musculature.

margin. The bones of the rear of the lower jaw appear to have been displaced relative to each other and details of the space between the body of the angular and the reflected lamina cannot be made out. However, it is evident that the major part of the reflected lamina lies well below the ventral margin of the jaw and that it reaches its greatest anteroposterior extent along its ventral border. The articular is similar to that of other dicynodonts and the rounded lateral and medial condyles are clearly distinguishable from each other. A short, stout, ventrally directed retroarticular process is present.

Diagnosis

Dicynodonts with a fully developed sliding contact between convex quadrate and articular condyles and with horny beaks on upper and lower jaws.

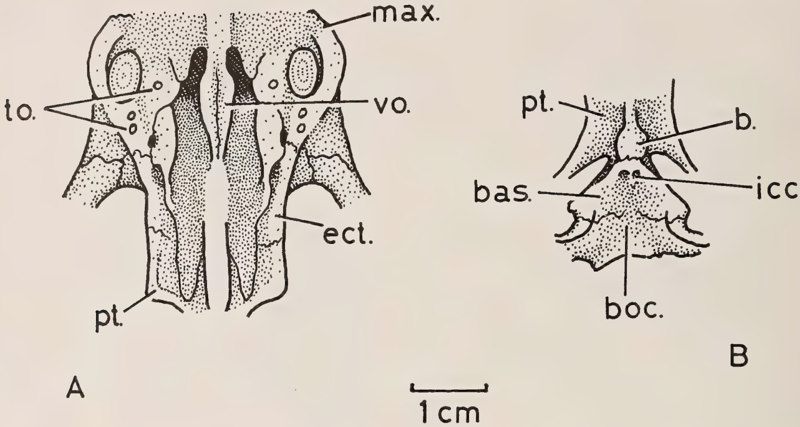

Fig. 7. *Eodicynodon oosthuizeni*. ROZ 11, from Zwartskraal, Prince Albert. A. Reconstructed palatal view of skull showing marginal position of posterior postcanine teeth. B. Basipterygoid region of skull showing bony boss on pterygoid keel.

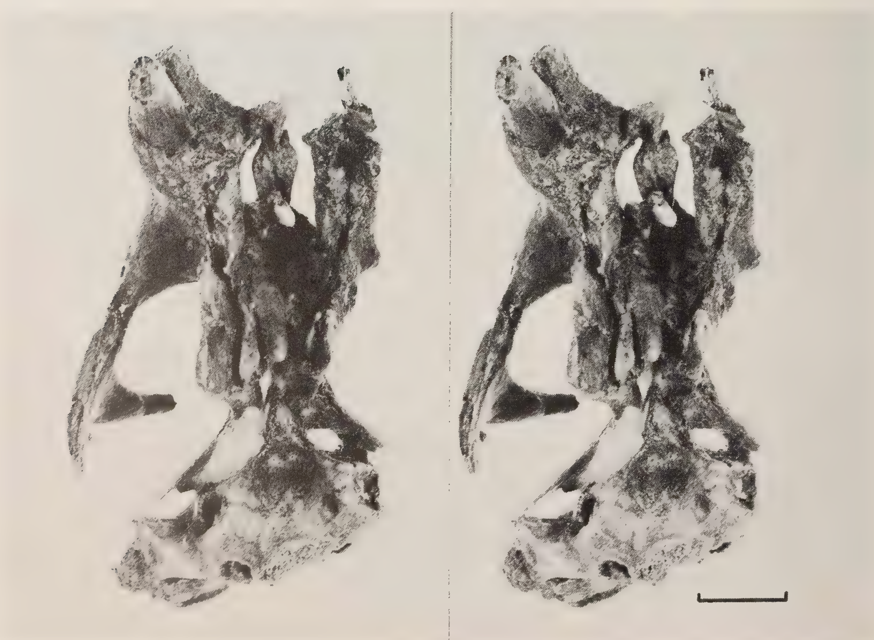

Fig. 8. *Eodicynodon oosthuizeni*. ROZ 11. Stereophotograph of skull in ventral view. Scale in cm.

Vomers paired, premaxillae paired. Strongly developed, ventrally directed lateral pterygoid process. No teeth on the anterior part of the premaxilla or on the anterior part of the dentary. Postcanine teeth present medial to the alveolar margin as well as on the alveolar margin itself. Palatal rim interrupted by deep cleft in front of maxillary tusk. Vomerine septum swollen behind the contact with the posterior premaxillary septum. Palatines bulbous and rugose. Median interpterygoidal crest enlarged to form a powerful ventral boss. Stapes pierced by stapedial foramen. Dentary with dorsally placed lateral ledge. Shallow groove in dorsal surface of the anterior part of the jaw ramus.

Genus *Endothiodon*, Owen, 1876

Type species *Endothiodon bathystoma* Owen, 1876

Type material

Anterior half of skull and lower jaw, BMNH R1646.

Locality

Sneeuwberg Range, Cape Province.

Stratigraphic horizon

Uncertain.

Remarks on the type specimen

Since Owen described the type specimen of *Endothiodon bathystoma*, various species have been added to the genus (see Haughton & Brink 1954). Cox (1964) has revised the genus and includes within it the genera *Endogomphodon*, *Esoterodon*, and *Emydochampsa*. His generic description will be used here with slight modifications based on the further examination of specimens of *Endothiodon uniseries* (BMNH R4044, BMNH R49414) and *Endothiodon* sp. (SAM–K1233) (Fig. 9).

Diagnosis

Dicynodonts of medium to large size (skull length 27,5–57,0 cm). Interorbital region wide. No postfrontal bone. Intertemporal bar narrow but enlarged around the region of the pineal foramen. Median groove running posterior to the pineal foramen towards the back of the skull.

In anterior view a deep median notch in front margin of the palate. In ventral view premaxillary secondary palate deeply vaulted. Tooth row placed far posteriorly and internally. Eight to eleven long teeth on each side, distal portions bearing anterior serrations when unworn. Anterior two teeth borne on premaxilla. Horn-covered groove lateral to tooth row. Trough in ventral surface of the median vomerine plate. Large palatine meeting the maxilla

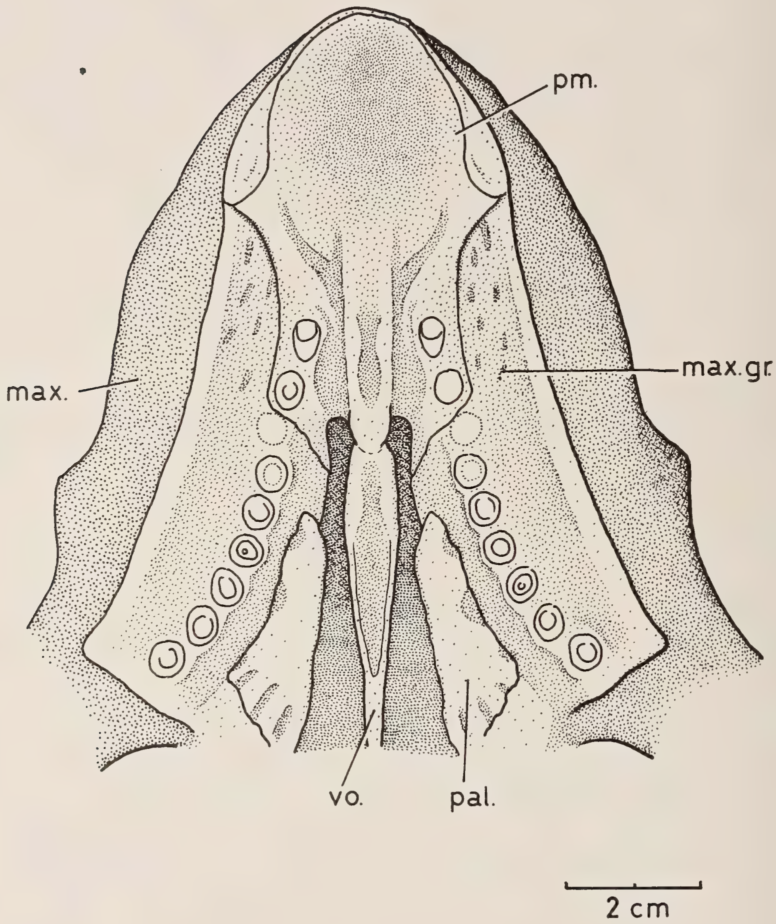

Fig. 9. *Endothiodon uniseries*. Type specimen BMNH 49414, from ?Beaufort West. Palatal view.

anteriorly, extending far back on to the internal surface of the pterygoid, but with little medial extension. Median ridge on posterior region of the pterygoids. Anterior pterygoid ramus very robust with modified lateral pterygoid process.

Anterior portion of the lower jaw toothless, prolonged into upward-curved and pointed beak fitting into vaulted palate. Dentary teeth long in a more or less straight line. Dorsal dentary trough lateral to tooth row. No dentary tables or lateral dentary shelf.

Genus *Pristerodon* Huxley, 1868

Type species *Pristerodon mackayi* Huxley, 1868

Type material

Skull and lower jaw BMNH R1810.

Locality

East London, Cape Province.

Stratigraphic horizon

Cistecephalus Zone.

Remarks on the type specimen

The type specimen is a poorly preserved, incomplete skull and lower jaw in intractable matrix (Fig. 10). On the skull roof little, apart from the preparietal, parietal and postfrontal, can be made out. The pineal foramen is placed

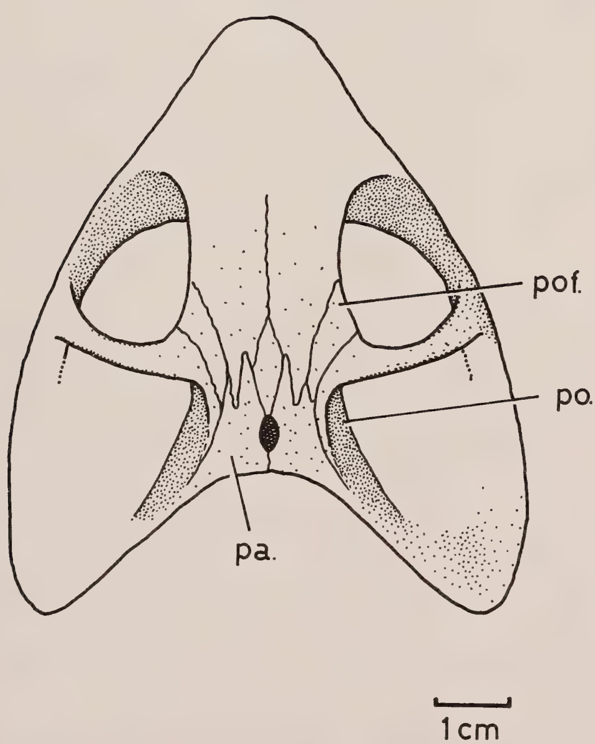

Fig. 10. *Pristerodon mackayi*. Type specimen BMNH R1650, from East London. Reconstructed dorsal view of skull.

relatively far back in the skull roof, and the preorbital region appears to have been fairly long. The intertemporal region is wide and formed mainly by the parietals. Canine tusks are absent.

Altogether nine small teeth are visible in the lower jaw. All the teeth are damaged and serrations are not visible.

Since the type specimen is so poorly preserved other species presently assigned to the genus were examined with a view to establishing a fuller generic diagnosis.

Description of Pristerodon raniceps

P. raniceps was described by Owen in 1876 as *Oudenodon raniceps*. It was referred to the genus *Pristerodon* by Broom (1915) on the basis of the presence of postcanine teeth. The type specimen consists of a skull and lower jaw (BMNH R1650) from East London (Fig. 11). While the bone is moderately well preserved, few sutures can be made out with certainty. The preparietal bone can be distinguished, and the pineal foramen is situated far back in the skull as in the type specimen of *P. mackayi*. The intertemporal region is broad, as in *P. mackayi*, and presumably formed mainly by the parietal bones. The palate is obscured by extremely hard matrix.

The lower jaw shows several important features. There is a broad lateral dentary shelf directly above the mandibular fenestra extending forward on the side of the dentary well beyond the anterior border of the fenestra. Six, possibly seven, posteriorly serrated teeth are visible in the jaw and are placed medially to a deep, thin-walled groove or sulcus in the dorsal edge of the dentary.

Description of Pristerodon whaitsi

P. whaitsi was described by Broom (1911) and is based on a skull (AMNH 5507) from Lemoenfontein, Beaufort West. The skull is laterally compressed and much of the dorsal skull roof in the interorbital and snout region is missing (Fig. 12). In the intertemporal region the parietals are widely exposed between the postorbitals and a postfrontal bone is present. The palate has suffered lateral distortion but certain features are nevertheless clear. The palatine bone is large, leaf-like and lies as a posterior extension of the premaxillary-maxillary secondary palate. Five small teeth are present medial to the canine tusk and lie in a straight line leading from an anterior medial position to a lateral position in line with the canine tusk. The posterior teeth in the row are situated on a platform of the maxilla, slightly lower than the level of the palatine and medial to the alveolor border. The posterior postcanine teeth lie close to the alveolar border.

In the lower jaw at least six functional teeth are present in a single row medial to a trough or sulcus in the dorsal border of the dentary. A large lateral dentary shelf is present and resembles that seen in *P. raniceps*.

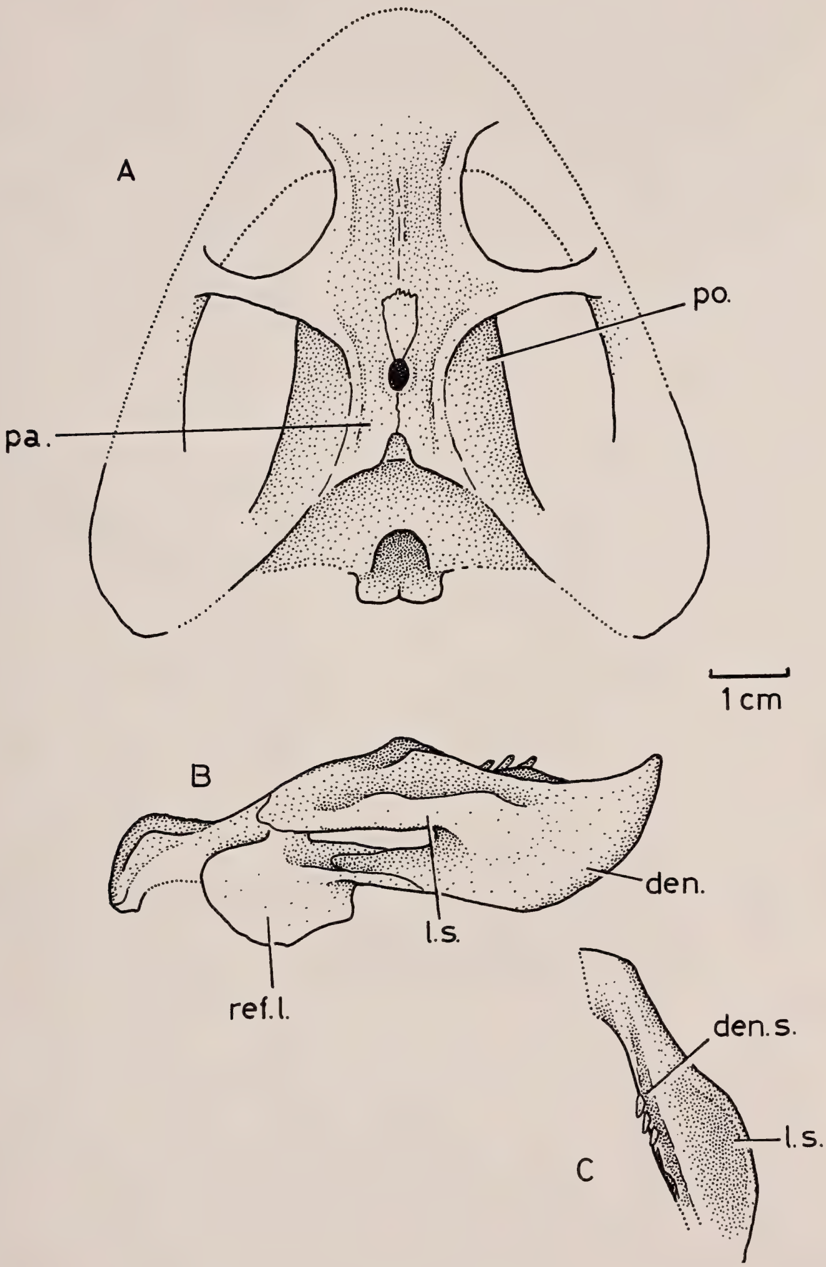

Fig. 11. *Pristerodon raniceps*. Type specimen BMNH R1650, from East London. A. Reconstructed dorsal view of skull. B–C. Lower jaw in lateral and dorsal views respectively.

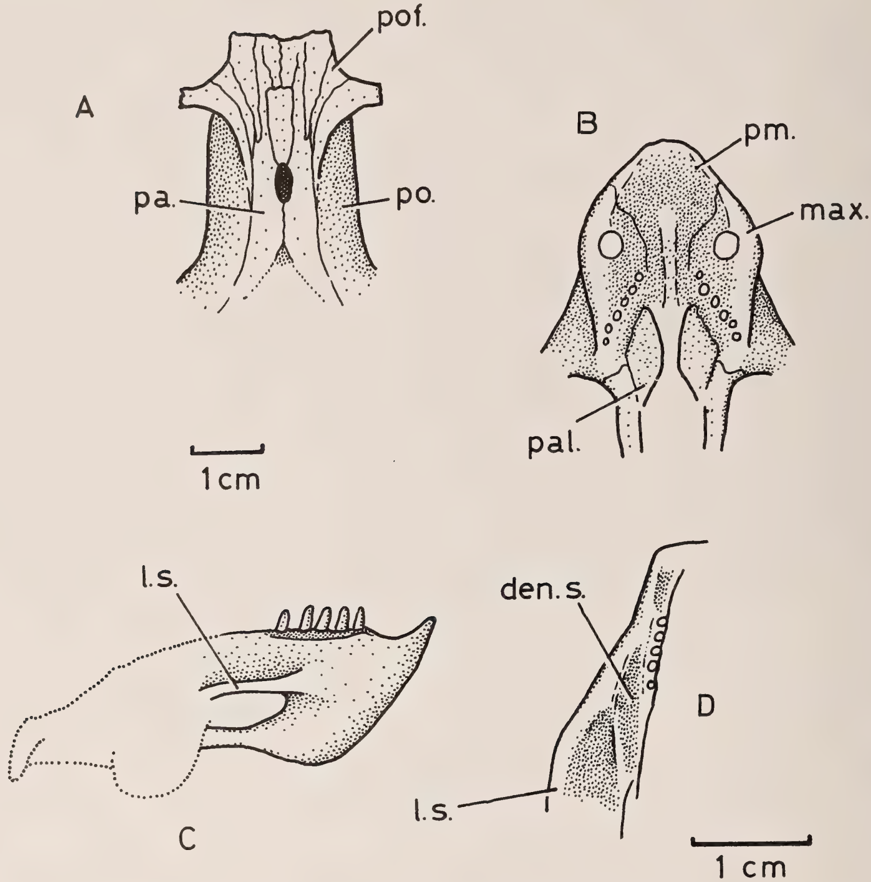

Fig. 12. *Pristerodon whaitsi*. Type specimen AMNH 5507, from Lemoenfontein, Beaufort West. A. Skull roof. B. Reconstructed palatal view. C–D. Lower jaw in lateral and dorsal view respectively.

Diagnosis

Formulation of a diagnosis for the genus *Pristerodon* is made difficult by the nature of the type specimen of *P. mackayi* in which only a minimal amount of morphological detail is visible. Ideally, in order to draw up a full generic diagnosis, it would be necessary to include additional specimens firmly assigned to the same species but yielding more morphological information. Unfortunately such specimens are not available, although type specimens of other species at present assigned to the same genus are available (Fig. 13). If the information from the type species and additional species is pooled, then a diagnosis can be formulated, but at the risk of including characters that may have only specific significance. The alternative is to declare the type a *nomen nudum* and to base the genus on the earliest described, best preserved speci-

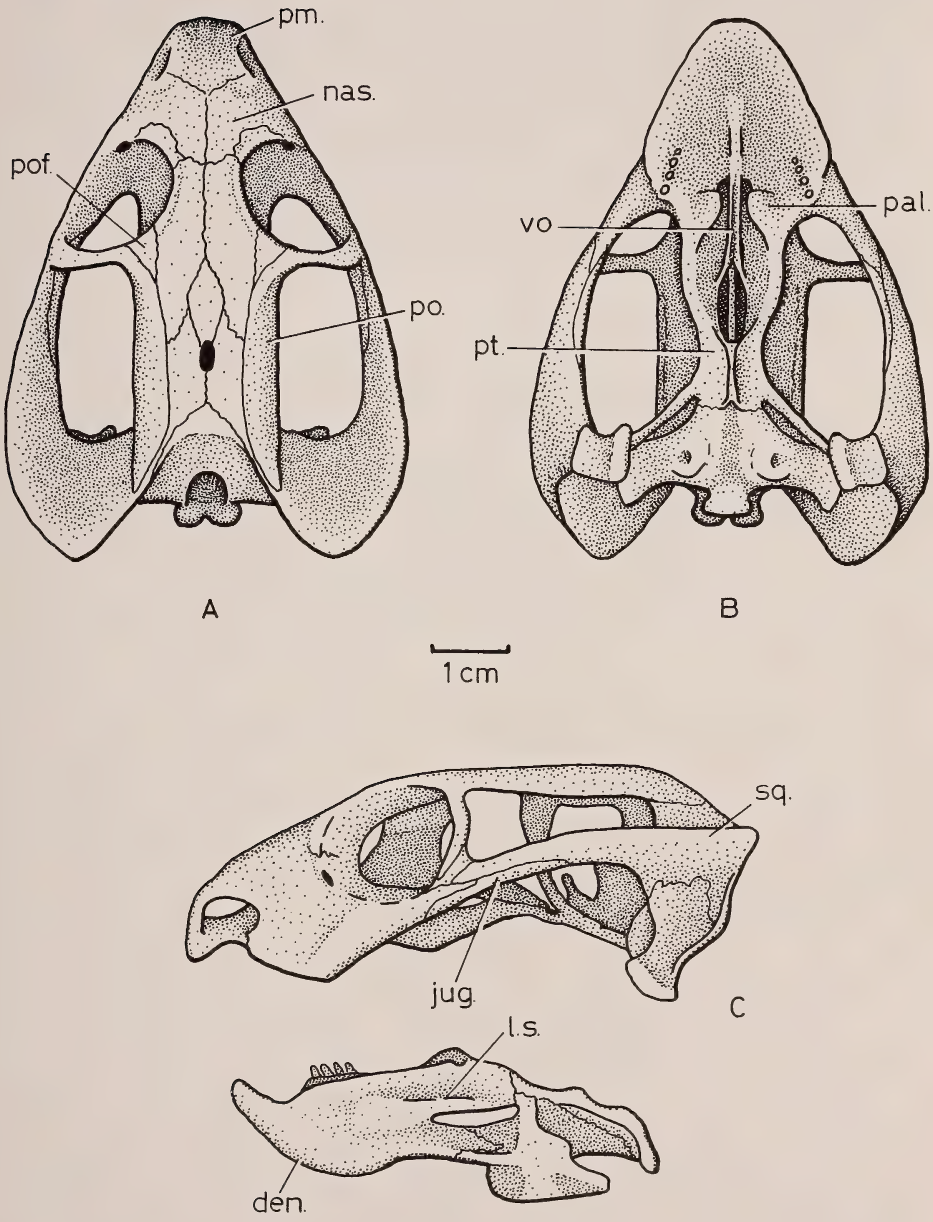

Fig. 13. *Pristerodon* sp. SAM–10153, from Dunedin, Beaufort West. A–B. Skull in dorsal and ventral views. C. Skull and lower jaw in lateral view.

men. In the interests of nomenclatural stability this alternative has not been followed here and it is proposed instead that *P. mackayi* remain the type species, and that the generic diagnosis be supplemented with information from the species *P. raniceps* and *P. whaitsi*. Where the characters included in the diagnosis are from either of the latter two species, the characters do not conflict with the condition found in *P. mackayi*, if verifiable. Any characters chosen that cannot be verified in the type species will be allowed to stand until it can be shown that the type species differs from the additional species in those characters.

This procedure has been explained in some detail since it is used elsewhere in the present work.

The revised generic diagnosis is as follows.

Small dicynodonts, with or without maxillary tusks. Intertemporal part of the skull roof broad, with wide parietal exposure. Palatines large and leaf-like, forming posterior extension of secondary palate surface. Interpterygoidal vacuity extending forward as a trough on to the rear of the vomerine septum. Median interpterygoid ridge continues anteriorly on to the ventral surface of the anterior pterygoidal process. Palatal rim unbroken by notches or embayments anterior to the tusk position. Postcanine teeth lie in an oblique row medial to a deep sulcus in dorsal edge of dentary. Dentary carries strong lateral dentary shelf above and in front of mandibular fenestra.

Genus *Tropidostoma* (Seeley, 1889)

Type species *Tropidostoma microtrema* (Seeley, 1889)

Type material

Occiput and part of skull roof, BMNH R868.

Locality

Tafelberg, Beaufort West, Cape Province.

Stratigraphic horizon

Cistecephalus Zone.

Remarks on the type specimen

Dicynodon microtrema was described by Seeley in 1889, based on the occiput and posterior part of the skull roof of BMNH R868 (Fig. 14B).

In the same paper Seeley also described *Tropidostoma dunni*, the posterior part of a skull (BMNH R866). From the description this appears to differ from *Dicynodon microtrema* mainly in the configuration of the lateral extension of the squamosal. In *Tropidostoma dunni* it extends vertically above the level of the postparietal region, while in *D. microtrema* the temporal region is high above the lateral extension.

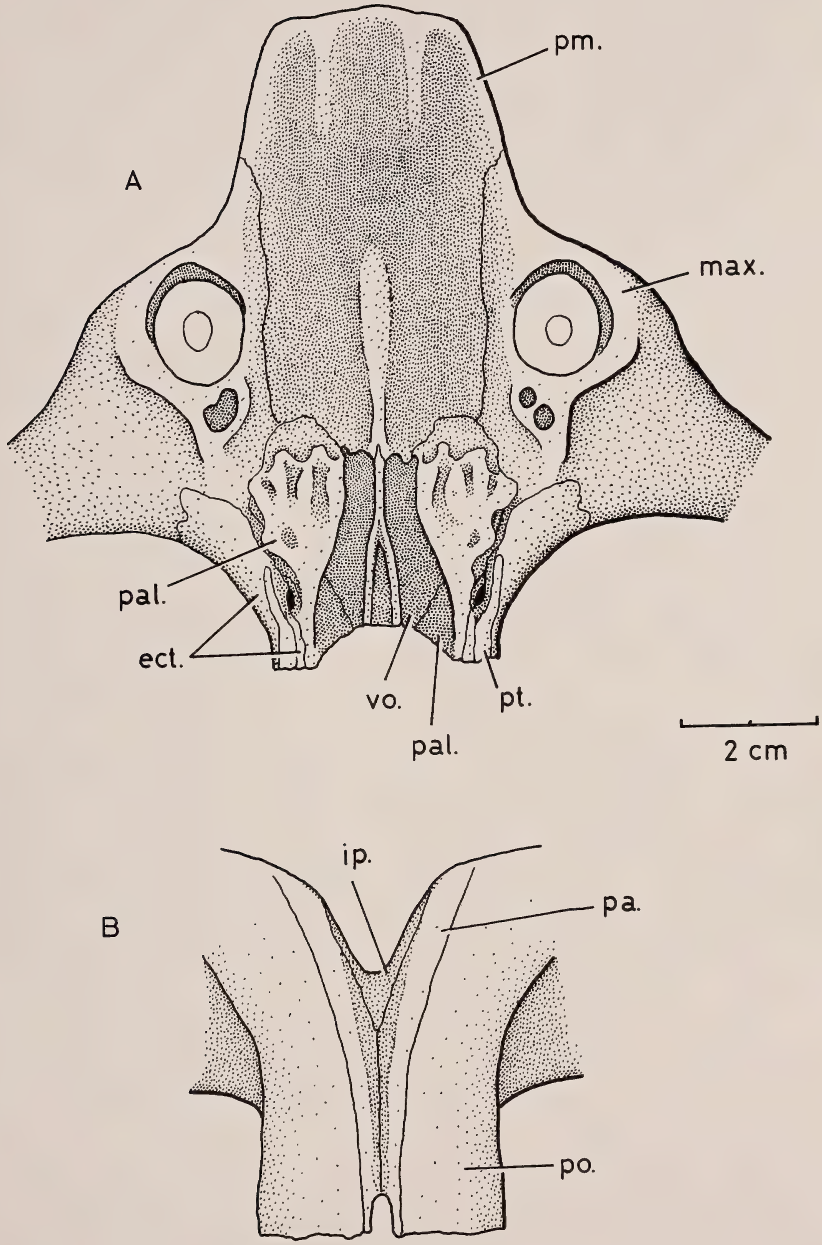

Fig. 14. A. *Tropidostoma microtrema*. BMNH R860, from Tafelberg, Beaufort West. Palatal view of specimen, showing empty sockets for postcanine teeth. B. *Tropidostoma microtrema*. Type specimen BMNH R868, from Tafelberg, Beaufort West. Dorsal view of the intertemporal region.

Broom (1915) referred new specimens from the Tafelberg locality to Seeley's *Dicynodon microtrema*. He found the new specimens to be characterized by the presence or absence of tusks (possibly a sexually dimorphic feature) and by small molars, which may be lost with age, behind the tusks or caniniform processes.

Broom considered that, since no *Dicynodon* specimen had postcanine teeth, the present forms should be referred to a new genus. He argued that *D. microtrema* was probably synonymous with *Tropidostoma dunni*, and therefore assigned the new Tafelberg specimens, as well as *D. microtrema*, to *T. microtrema*. One of the new specimens, BMNH R860 (Fig. 14A), formed the basis of Broom's description of *T. microtrema*: palatal premaxillary ridges are present; the postcanine teeth on the maxilla are striated; the septomaxilla lies within the nostril; the nasals bear thickened nasal bosses; the postorbitals and parietals are developed into a pair of lateral crests with a groove between them; the palatal portion of the premaxilla is large; the lower border of the prevomer is developed as a pair of ridges; and the palatines are large.

Re-examination of this specimen by the present authors showed that the 'prevomer lower border plates' actually represent the sides of a trough in the ventral edge of the vomerine septum, and that a sharp crest is present posterior to the tusk or caniniform process.

Broom (1932) discussed *Tropidostoma microtrema* and again drew attention to the encroachment of the postorbitals on the parietals, and the deep furrow present between the upper edges of the parietals behind the pineal opening. Broom's figure shows a trough in the ventral edge of the vomer.

In Watson's (1948) description of *Tropidostoma* he mentioned three ridges on the palatal part of the premaxilla and a canine tusk and two small circular postcanine teeth on each side. The anterior part of the palatine extends towards the midline and was described as being relatively small, although his figure 13 shows it to be extensive. A long interpterygoidal vacuity is shown. Watson's specimen (D. M. S. Watson Collection R48) has an associated lower jaw. The dorsal surface of the dentary was described as being divided into three grooves, but the two outer grooves are actually shallow troughs borne on dentary tables. Watson noted a groove in the upper surface of the dentary ramus and five teeth in a single series lying lingual to the dentary groove.

Additional undescribed material has been examined by the present authors. BMNH R6963, a specimen of *Tropidostoma* sp. with a lower jaw associated, shows a dentary table bearing a shallow trough, a dentary groove or sulcus with teeth lying in a row lingual to the sulcus, and a deep median symphysial trough (Fig. 15).

SAM-10681, a skull of *Tropidostoma* sp., shows a pinched intertemporal region with a furrow between the parietals, tusks, small nasal bones, nostrils placed high in the snout, a crest on the alveolar border posterior to the tusk, postcanine teeth posterior to the tusk and situated close to the alveolar border, a short vomerine trough, large palatines, and a long interpterygoid vacuity.

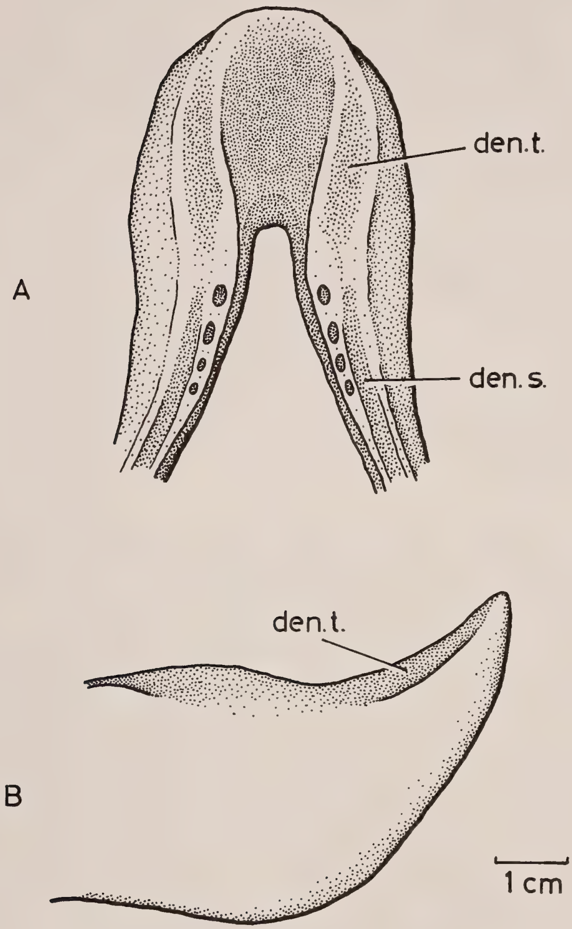

Fig. 15. *Tropidostoma* sp. BMNH R6963. A–B. Anterior portion of lower jaw in dorsal and lateral views.

For the present it is felt justifiable to include information from all the above specimens in a generic diagnosis.

Diagnosis

Medium-sized dicynodonts with or without tusks. Alveolar border behind tusk or caniniform process forms a sharp postcanine crest that may or may not bear teeth. Palatine large with bulbous anterior palatal portion. Vomer bears trough (which may be short) along ventral edge. Interpterygoidal vacuity long. Nostril set high in the snout. Nasals bear weak bosses. Pinched intertemporal

region. Postorbitals overlie parietals and form sides of a deep groove or furrow leading backward from the pineal foramen.

Lower jaw with weak dentary tables. Dorsal surface of dentary table bears trough. Deep median trough between dentary tables. Dentary sulcus present. Few postcanine teeth present in a row in longitudinal groove lingual to dentary sulcus. Weak lateral dentary shelf.

Related genera

Keyser (1973) redescribed *Cteniosaurus platyceps* Broom and assigned it to *Tropidostoma microtrema*. The characters that Keyser regarded as common to the two forms are a similar configuration of the bones of the skull surface, and the nostril placed high in the skull. Other similarities that can be detected are: weak nasal bosses, a long interpterygoidal vacuity, a few small postcanine teeth, a sharp postcanine crest, and extensive palatines that have an inflated posterior part and a smooth anterior part that meets the premaxilla.

A very weathered jaw ramus is the only lower jaw material available for *Cteniosaurus*.

Unlike previously described material that has been assigned to *Tropidostoma*, *Cteniosaurus* has a wide intertemporal region. This is not pinched and does not show the deep median furrow leading backward from the pineal foramen. In this respect it resembles specimens such as the type specimen (SAM–2356) of *Dicynodon rogersi* Broom & Haughton, 1917, and a similar as yet undescribed specimen SAM–B390, which have postcanine teeth but wide intertemporal regions. It is considered here that the state of the intertemporal region is a meaningful character since its morphology will impose constraints on the organization of the jaw musculature. It is therefore felt that *Cteniosaurus* should not be included in the genus *Tropidostoma*. Both *Tropidostoma* and *Cteniosaurus* may be regarded as early *Oudenodon*-like forms, which in some cases retain postcanine teeth. Features such as the weak nasal bosses, the long interpterygoidal vacuity, the sharp postcanine crest, and the shape of the palatine all ally *Cteniosaurus* and *Tropidostoma* with *Oudenodon* (see p. 223).

Although *Tropidostoma*, *Cteniosaurus*, and *Oudenodon* are clearly related, it is not possible at this stage to determine the exact relationships of the three genera.

Genus *Rhachiocephalus* (Owen, 1876)

Type species *Rhachiocephalus magnus* (Owen, 1876)

Type material

Incomplete skull BMNH 36252.

Locality

Brak River, Fort Beaufort, Cape Province.

Stratigraphic horizon

Cistecephalus Zone.

Remarks on the type specimen

Seeley (1898) erected the genus *Rhachiocephalus* for *Oudenodon*-like (i.e. tuskless) forms with a narrow intertemporal region. *Oudenodon magnus* Owen, 1876, was made the type species and transferred to the genus *Rhachiocephalus*.

The type specimen is tuskless and fairly large (skull length approximately 50 cm). Nasal bosses are present. The intertemporal region is narrow and drawn up into a crest and the parietals are only slightly exposed on the skull roof. The pineal foramen is situated in the middle of a bony boss. Few details of the palate can be distinguished, but it is possible that an interpterygoidal crest exists. There is a median palatal premaxillary ridge and the palatines are large. In describing the same specimen in 1932, Broom notes that there are no postfrontal bones.

Remarks on other species

Two additional species of *Rhachiocephalus* have been described. *R. angusticeps*, described by Broom (1937), is an incomplete skull in the Transvaal Museum (no. 1489). The skull is large and tuskless, has a narrow intertemporal region with a crest and a pineal foramen situated in a bony boss. The description given by Broom does not permit closer comparison, but there seem to be no obvious features separating *R. angusticeps* and *R. magnus* at either the generic or specific level. Since the aim of the present work is to attempt to formulate generic diagnoses, not to revise dicynodonts at the specific level, for the moment both species will be allowed to stand.

Rhachiocephalus dubius (SAM–11313) from the Luangwa Valley, Zambia, was described by Boonstra (1938). Although the type specimen has a narrow intertemporal region, re-examination shows that this form is tusked. There is no pineal boss, instead the skull roof in this region is shallowly concave. There are nasal bosses, but these are very elongate, and may have been affected by crushing.

Since *R. dubius* does not show two of the main characteristics expected in the genus *Rhachiocephalus*, namely tusklessness and a pineal boss, it cannot remain in that genus. Keyser & Cruickshank (1979) make *R. dubius* the basis of their new genus *Odontocyclops*. This will be discussed later (p. 238), when it will be argued that certain of the large tusked forms, amongst them '*Odontocyclops*' *dubius*, may simply be larger members of one of the *Dicynodon* species such as *D. leoniceps*.

Diagnosis

Large tuskless dicynodonts. Nasal bosses present. Intertemporal region narrow and drawn up into a crest. Parietals hardly exposed on skull roof. Pineal

foramen situated in a bony boss. Median palatal premaxillary ridge. Palatines large. No postfrontal bones.

Genus *Eocyclops* Broom, 1913

Type species *Eocyclops longus* Broom, 1913

Type material

Skull in AMNH.

Locality

Grootvlei, Paardekraal, Beaufort West, Cape Province.

Stratigraphic horizon

Cistecephalus Zone.

Remarks on type specimen

As described by Broom (1913), *Eocyclops longus* shows the following features: skull length is approximately 44 cm; nasal bosses are present; smaller bosses are present over the orbits; the large pineal foramen is surrounded by the thickened, ring-like parietal; the preparietal is absent; the postfrontal extends along the postorbital bar; the postorbitals almost overlap the parietals in the intertemporal region; tusks are absent; there is a feeble caniniform process.

Broom (1913) considered that *Oudenodon magnus* Owen, 1876, belonged to the new genus, but it was later found to possess a preparietal. *O. magnus* eventually became the genotype for *Rhachiocephalus*, as described above.

From the published descriptions the only feature that separates *Rhachiocephalus* and *Eocyclops* is the apparent lack of a preparietal in the latter. This may be an unreliable feature for taxonomic purposes, as frequently it is difficult to interpret the sutures around or within the pineal boss. Haughton (1917), in describing what he considered to be a specimen of *Eocyclops longus* with a preparietal, obviously set little store on this as a distinguishing feature. (Even so, Broom later reassigned this specimen to a new genus, *Megacyclops*.) A specimen in the University Museum, Oxford (TSK 23), which is undoubtedly *Eocyclops*, shows a ring-like preparietal surrounding the pineal foramen. However it is evident that this bone is the preparietal only because the specimen is broken through the pineal foramen and sutures are clearly visible. It is possible, therefore, that Broom mistook a ring-like preparietal for the parietal.

Until the type specimen of *Eocyclops longus* can be re-examined in detail it cannot be stated with confidence whether a preparietal is present or not. However, in view of other similarities it is considered here that, even if a preparietal is absent from the skull roof, this is not a character that necessitates generic separation, and it is recommended that *Eocyclops longus* be accommodated in the genus *Rhachiocephalus*.

Genus *Platycyclops* Broom, 1932

Type species *Platycyclops haughtoni* Broom, 1932

Type material

Skull SAM–8750.

Locality

Doornplaas, Graaff-Reinet, Cape Province.

Stratigraphic horizon

Cistecephalus Zone.

Remarks on the type specimen

Broom described *Platycyclops haughtoni* in 1932 from a large, moderately flat skull without tusks. The preorbital region is wide. There are large postorbitals and narrow parietals. The preparietal is crescentic and forms the front half of a pineal boss.

Broom stated that a postfrontal is not present although Haughton & Brink (1954) stated correctly that there is a very large and distinct postfrontal.

The type specimen was re-examined and the following additional information gained. The pineal foramen faces anterodorsally. Behind it there is some parietal exposure, but the postorbitals close over the parietals posteriorly. As preserved, the intertemporal region is wide and flat because the postorbitals, instead of sloping ventrolaterally, face directly dorsally. This could be due in part to post-mortem deformation.

The jugal has a short spur, which extends up into the postorbital bar. There are small nasal bosses. The nostril is recessed with a definite posterior margin and does not grade imperceptibly into the surface of the snout. The postfrontal extends along the postorbital bar.

On the palate there is a strong postcaniniform crest. There are two anterior palatal premaxillary ridges and a median posterior ridge. The vomer does not bear a trough along its ventral edge and there is a fairly short interpterygoidal vacuity. The palatines have a large bulbous anterior exposure.

Other features are as Broom described them, except that a postfrontal is present.

Remarks on other species

Broom (1940) described two additional species of *Platycyclops*, *P. latirhinus* and *P. rubidgei*. These conform to Broom's diagnosis of the genus but show some variation in the intertemporal region. In *P. latirhinus* this region is moderately wide, although the parietals are still overlapped by the postorbitals to a great extent. In *P. rubidgei* the intertemporal region is narrower. Such variation is probably tolerable within a species, almost certainly within a genus, since the important diagnostic feature here is whether the parietals are overlap-

ped by the postorbitals, forming a structure approaching a sagittal crest. Absolute width is probably diagnostically unimportant, as it may vary with absolute skull size. The degree to which overlapping occurs may be age- or sex-dependent, leading to the variation seen.

In *P. pricei* (Broom & George 1950) the postorbitals approach each other over the parietals, although they do not meet. In *P. acutirostris* (Broom & George 1950) the postorbitals meet over the parietals.

In other features these four specimens conform to the generic description.

There seems to be little in Broom's original description to warrant erecting a new genus for these forms apart from the condition of the preparietal—absent in *Eocyclops*, present in *Platycyclops*. However, this distinction becomes irrelevant in the present work since *Eocyclops* has been referred to the genus *Rhachiocephalus* where the preparietal is quite similar to that of *Platycyclops*. It is therefore recommended that *Platycyclops* also be included in the genus *Rhachiocephalus*.

Genus *Neomegacyclops* Boonstra, 1958

Type species *Neomegacyclops whaitsi* (Broom, 1931)

Type material

Part of the skull roof, postorbital bar and part of the zygoma SAM–3425.

Locality

Graaff-Reinet, Cape Province.

Stratigraphic horizon

Uncertain.

Remarks on the type specimen

In 1917 Haughton described a partial dicynodont skull that, although possessing a preparietal, he considered to be sufficiently similar in other respects to *Eocyclops longus* to be included in that genus and species. The preparietal of the specimen forms most of a boss round the pineal foramen. The parietals have a very small exposure between the overlapping postorbitals. There is a small nasal boss and a thickened postfrontal. Haughton reported that there was no septomaxilla showing on the surface of the snout. The reconstructed length of the skull would be approximately 50 cm.

Broom (1931) renamed the specimen *Megacyclops whaitsi* because the pineal opening is small and the preparietal and parietal form a huge, rounded pineal boss. Boonstra (1953) subsequently erected the new genus *Neomegacyclops* for the specimen since the name *Megacyclops* was found to be preoccupied.

Re-examination of the type specimen reveals few other features of diagnostic significance since the palate is unprepared. The nostril has a definite

posterior margin. The orbit is triangular and the postfrontal extends into the postorbital bar. On the ventral surface of the distal part of the postorbital bar there is a smooth recess that seems to be continuous with a smooth recess on the posterior dorsal surface of the suborbital bar. These may be for muscle attachment, in which case the extension of the postfrontal into the postorbital bar may be a means of strengthening it or its connection with the skull roof.

Another specimen, SAM–K1393, has certain features in common with *Neomegacyclops whaitsi* and the other tuskless forms described above. There is a boss mostly posterior to the pineal foramen formed by the parietals. A preparietal is present. The postorbitals overlap the parietals closely in the intertemporal region. There are nasal bosses and prefrontal thickenings. There is a median crest on the nasal and frontal bones, but this may be the result of lateral compression. The nostril has a definite posterior margin. The postfrontal extends into the postorbital bar. There is a recess on the ventral surface of the distal part of the postorbital bar and also on the posterior dorsal surface of the suborbital bar. The jugal forms part of the posterior surface of the postorbital bar.

Additional features of this specimen are a median interpterygoid crest, absence of a vomerine trough, absence of tusks, a sharp postcaniniform crest and a palatine with a bulbous anterior portion.

It has not been possible to find any features in the type specimen of *Neomegacyclops whaitsi*, or in a related species *Neomegacyclops rugosus* (Haughton 1932), or in the specimen SAM–K1393 described above that would debar any of these forms from the genus *Rhachiocephalus*. It is therefore suggested that these forms should be included in that genus.

Note on the large tuskless dicynodonts

The genus *Rhachiocephalus* is considered to be a well-defined, distinct taxon. The genera *Eocyclops*, *Platycyclops* and *Neomegacyclops* are synonymous with *Rhachiocephalus*. *Pelorocyclops* (Broom 1932) and *Kitchingia* (Broom & George 1950), which are not discussed here, can probably also be accommodated within this genus.

Genus *Oudenodon* Owen, 1860

Type species *Oudenodon baini* Owen, 1860

Type material

Skull lacking lower jaw, BMNH 36232.

Locality

Near Fort Beaufort, Cape Province.

Stratigraphic horizon

Uncertain.

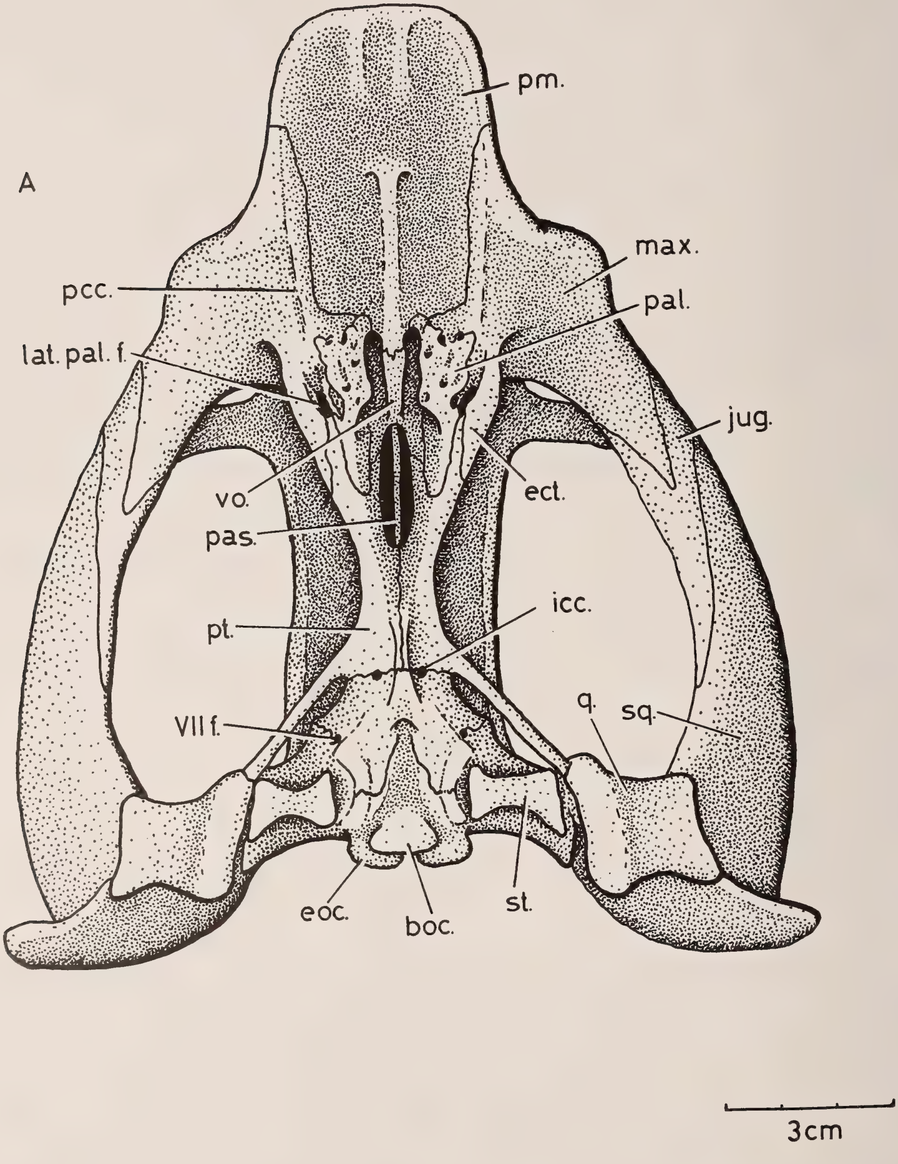

Fig. 16. *Oudenodon baini*. Type specimen BMNH 36232, from 'near Fort Beaufort'. Skull in ventral view.

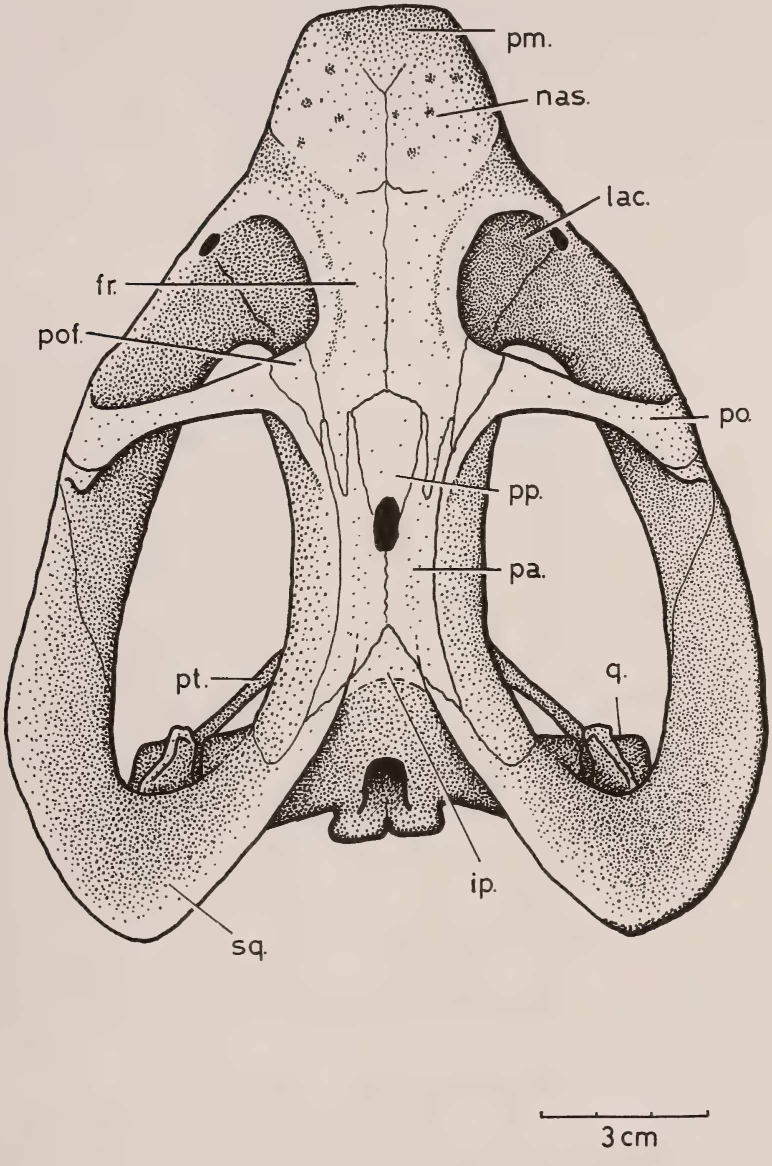

Fig. 17. *Oudenodon baini*. Type specimen BMNH 36232. Skull in dorsal view.

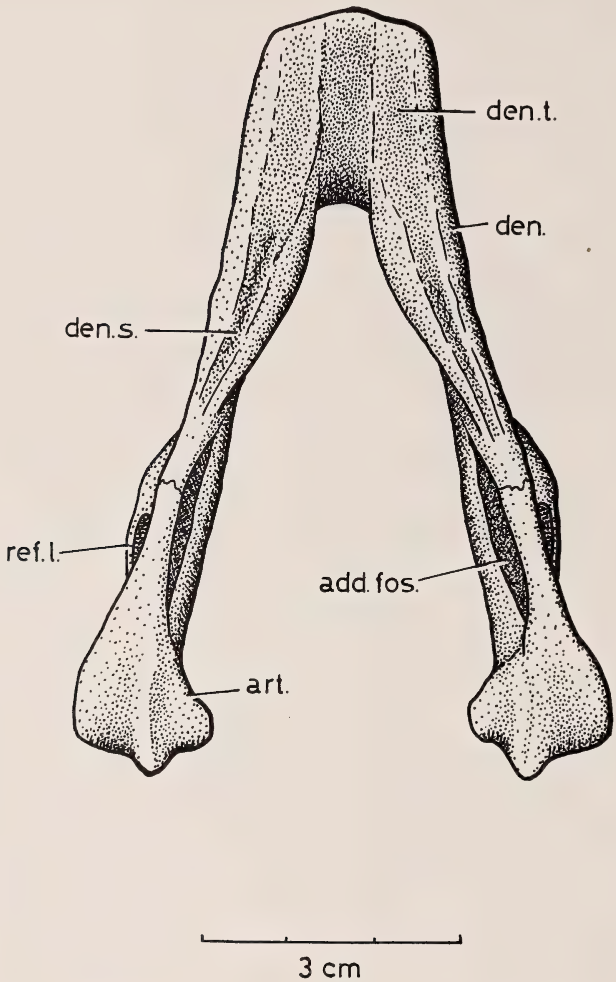

Fig. 18. *Oudenodon* sp. SAM–6045, from Houd Constant, Graaff-Reinet. Lower jaw in dorsal view.

Diagnosis

The genus *Oudenodon* (Figs 16–18) has recently been reviewed and illustrated by Cluver & Hotton (1981) and their diagnosis with slight modification will be used here.

Medium-sized to large dicynodonts (skull length ranging from 100 mm to over 300 mm). Teeth lacking in both upper and lower jaws. Postorbitals well separated on skull roof by parietals. Septomaxilla recessed within external

naris, lacrimal in some species extends forward above maxilla to posterior margin of naris. Nasal forms boss over naris. Maxilla carries weak caniniform process, with sharp-edged posterior crest. Palatal part of palatine divided into an inflated posterior area, and a smooth anterior part that meets the premaxilla. Vomers form short septum in anterior part of interpterygoidal fossa. Ectopterygoid large with palatal exposure, pterygoid does not contact maxilla. Dentaries with narrow dentary tables, dorsal edge of dentary with deep sulcus. Dorsal process on rear of dentary weak or absent. Weak lateral dentary shelf above large mandibular fenestra.

Genus *Aulacephalodon* (Owen, 1844)

Type species *Aulacephalodon baini* (Owen, 1844)

Type material

Skull BMNH 36238.

Locality

Fort Beaufort, Cape Province.

Stratigraphic horizon

Uncertain.

Note on the spelling of generic name

Seeley (1898) originally erected this taxon as a subgenus of *Dicynodon* with the following spelling: *Aulacephalodon*. Broom (1932) raised the subgenus to the generic level and for no apparent reason changed the spelling to *Aulacocephalodon*. Both Keyser (1969) and Tollman & Grine (1980) have discussed the validity of this and conclude that *Aulacephalodon* is the correct generic name; this will be used here throughout.

Remarks on the type specimen

In 1898 Seeley erected the subgenus *Aulacephalodon* for members of the genus *Dicynodon* (i.e. tusked forms) that were broad headed and short snouted. *Dicynodon baini* Owen, 1844, became the type species of the new genus.

Aulacephalodon baini is described by Owen (1844, 1876) as a skull slightly wider than long with a wide intertemporal region and exposed parietals. The pineal foramen is surrounded by a boss. The postorbitals in the intertemporal region are steep sided and there is a boss on the posterior surface of the postorbital bar. Tusks are present. The anterior pterygoid rami are widely divergent.

The snout and palate are not well preserved in the type specimen and little detail can be made out. In his *Catalogue* Owen (1876) also described *Dicynodon tigriceps*, which Seeley later assigned to *Aulacephalodon*. This specimen

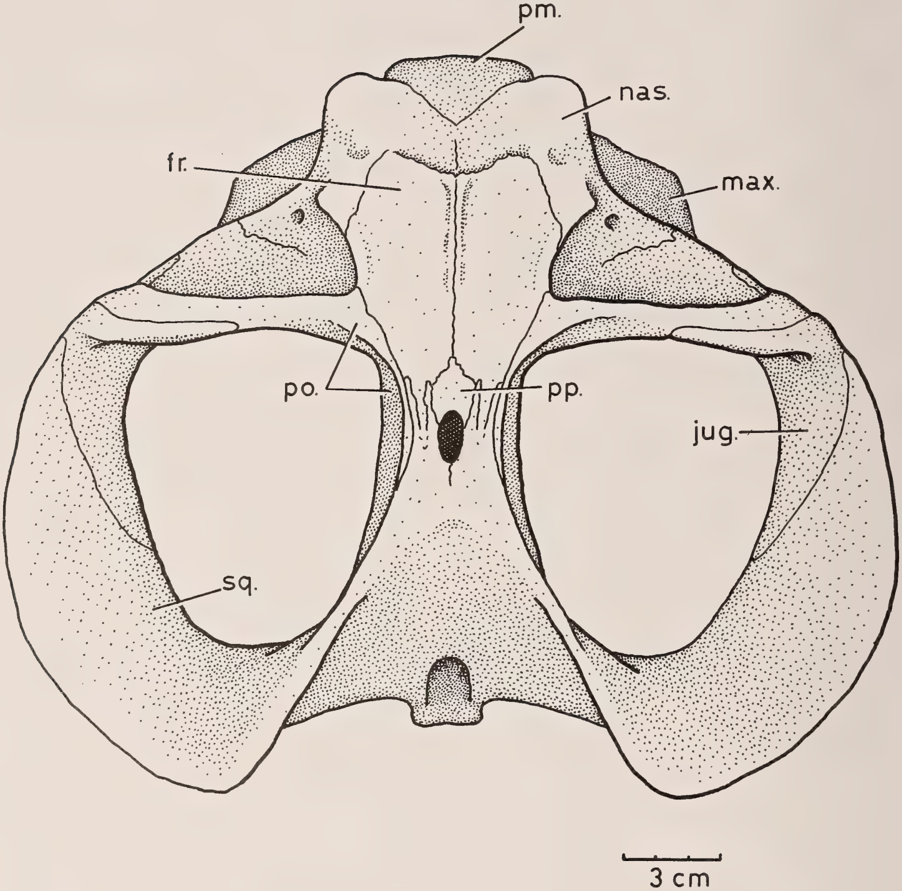

Fig. 19. *Aulacephalodon laticeps*. Type specimen AMNH 5564, from Grootvlei, Beaufort West. Skull in dorsal view.

(BMNH 36235) is better preserved and, in addition to the features described above, it has prefrontal and nasal bosses, a ridge across the snout between the prefrontal bosses, and a boss on the jugal of the zygoma, lying just posterior to the postorbital bar. These features cannot be verified on the more poorly preserved *A. baini*. The postorbital boss is not present in *A. tigriceps* and may therefore represent a specific feature of *A. baini*, so this feature should not be included in a generic description of *Aulacephalodon*. Otherwise these features

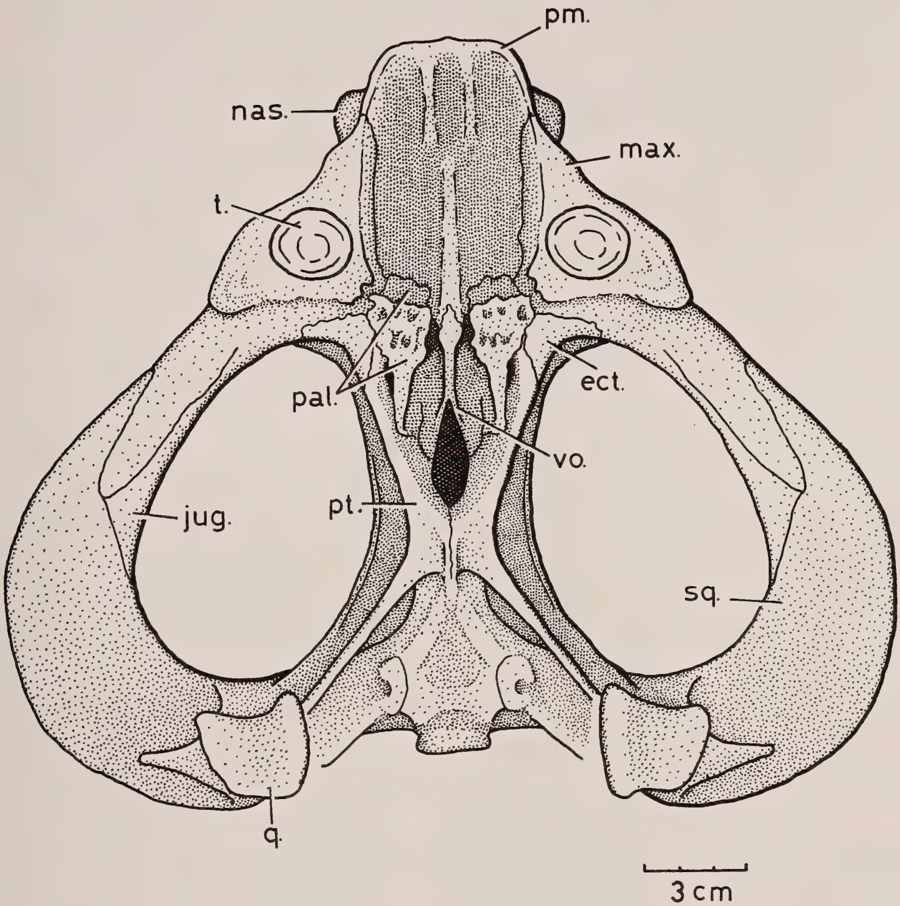

Fig. 20. *Aulacephalodon laticeps*. Type specimen AMNH 5564. Skull in ventral view.

may be combined to give a generic diagnosis of *Aulacephalodon*.

Various other species have been assigned to the genus (see Haughton & Brink 1954). In a recent review Keyser (1972) concluded that so-called specific differences are actually due to age and he considered that most of the species may be invalid. In their study on a large sample of *Aulacephalodon* skulls, Tollman, Grine & Hahn (1980) concluded that biometrical (allometric) methods indicate that only one species (*Aulacephalodon baini*) was present during the southern African Permian, and that this species showed clear sexual dimorphism and ontogenetic variation.

Description of additional material

The type specimen of *Aulacephalodon luckhoffi* Broom, 1937 (SAM–K1231) is the greater part of a skull lacking the lower jaw. It is in a reasonable state of preservation. In this specimen the skull is slightly longer than wide, but otherwise all diagnostic characters named above are present. In addition, *A. luckhoffi* shows a steep postorbital region that is drawn up into a low dorsal ridge. The postorbital overhangs the side wall of the braincase and forms a well-defined recess beneath the skull roof. The boss on the zygoma is well marked. The nostril is deeply recessed and has a definite posterior margin. The postfrontal bone is absent. A ridge on the premaxilla runs from the postero-dorsal corner of the nostril to the maxillary rim. There is a moderately large interpterygoidal vacuity. The median vomerine plate does not bear a trough. The palatines are extensive and have an anterior bulbous portion. There are two anterior premaxillary palatal ridges as well as the single posterior pre-maxillary palatal ridge. There is no postcaniniform crest.

The type specimen of *Aulacephalodon laticeps* (Broom, 1912) (AMNH 5564) is another good skull (without the lower jaw) in which the palate has been prepared recently (Figs 19–20). This specimen shows all the features described above, where verifiable, with only some minor modifications such as the prefrontal boss being weak. In addition, *A. laticeps* exhibits a jugal that bears a high process abutting against the postorbital posteriorly and extending far up the postorbital bar. There is also a relatively prominent interpterygoid crest.

Several undescribed specimens in the South African Museum (SAM–10053, SAM–10021 and SAM–K6064) have been examined and found to exhibit all characters noted above wherever the material permits investigation.

SAM–K6064 has a lower jaw *in situ*. This specimen is well preserved but unprepared. However, the form of the lower jaw is apparent. The dentary symphysis is massive and very deep. Posterior to the symphysis the depth of the jaw decreases to approximately one-third that of the symphysis. A typical dicynodont lower jaw condyle is present. At approximately one-third of the length of the jaw from the anterior end a lateral dentary shelf arises. Its length is also approximately one-third the length of the jaw. The shelf is directed ventrally so that it occludes the mandibular fenestra. A dorsal dentary sulcus is present.

Diagnosis

If the information from the foregoing specimens is pooled in the manner described earlier (p. 212) the following diagnosis can be formulated.

Medium-sized, tusked dicynodonts with a wide intertemporal region. Parietals exposed on skull roof. Pineal foramen surrounded by a boss. Postorbitals in intertemporal region steep sided and drawn up into ridge dorsally. Postorbitals overhang side wall of braincase forming recess beneath skull roof on each side. Boss on jugal of zygoma. Jugal has tall, dorsal process extending far

up postorbital bar. Prefrontal and nasal bosses. No postfrontal bone. Nostril is deeply recessed and has a definite posterior margin. Ridge on maxilla posterior to nostril.

Interpterygoidal vacuity moderately long. Ventral edge of vomerine plate without trough. Palatines bulbous. No postcaniniform crest.

Massive dentary symphysis with dentary tables. Lateral dentary shelf occludes mandibular fenestra. Dentary sulcus present.

Related genera

It may be possible to refer *Digalodon* (Broom & Robinson 1948) to this genus. This is based on a small specimen that generally conforms to the generic diagnosis except that the maxillary rim is cut upward in front of the canine tusk. It may prove to be either a distinct genus closely related to *Aulacephalodon* or a distinct species of that genus.

Genus *Pelanomodon* Broom, 1938

Type species *Pelanomodon rubidgei* Broom, 1938

Type material

Skull, Rubidge Collection 10.

Locality

Kareelaagte, Graaff-Reinet, Cape Province.

Stratigraphic horizon

Daptocephalus Zone.

Remarks on the type specimen

In Broom's (1938) original description, *Pelanomodon rubidgei* is characterized by the absence of tusks, the saddle-backed skull with beak folded down on the rest of the skull, the marked upwardly directed nasal bosses, smaller horn-like bosses on the prefrontals, little trace of a postfrontal, the small boss on the postorbital bar, the small preparietal almost entirely in front of the pineal foramen, the broad, flat parietals that produce the wide intertemporal region, and the large squamosals which flare out posterodorsally.

Remarks on additional specimens

In the same publication Broom (1938) mentioned *Aulacephalodon moschops* and considered that, since it was tuskless, it ought to be placed in another genus. Haughton & Brink (1954) assigned it to *Pelanomodon*.

Pelanomodon moschops (AMNH 5325, Figs 21–22) has the following features in addition to those described above: the postorbital in the intertemporal region is steep sided, there is a ridge across the snout between the prefrontal bosses, there is a smoothly recessed nostril, a labial fossa is present,

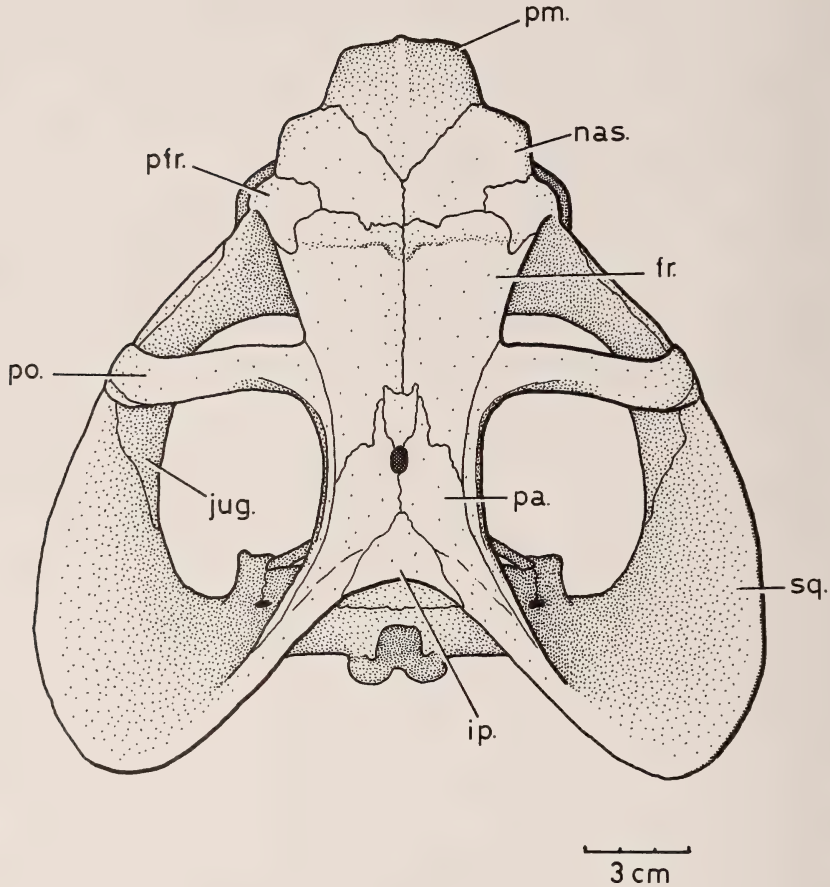

Fig. 21. *Pelanomodon moschops*. Type specimen AMNH 5325, from Oudeberg, Graaff-Reinet. Skull in dorsal view.

the interpterygoidal vacuity is relatively short, the palatines are large and the anterior portion is not bulbous but slopes slightly to meet the premaxilla, a very slight postcaniniform crest is present, the jugal boss, vomerine trough and interpterygoid crest are all absent.

A lower jaw for *Pelanomodon* is not known.

Diagnosis

Taking into account features from the above specimens, the following diagnosis may be formulated.

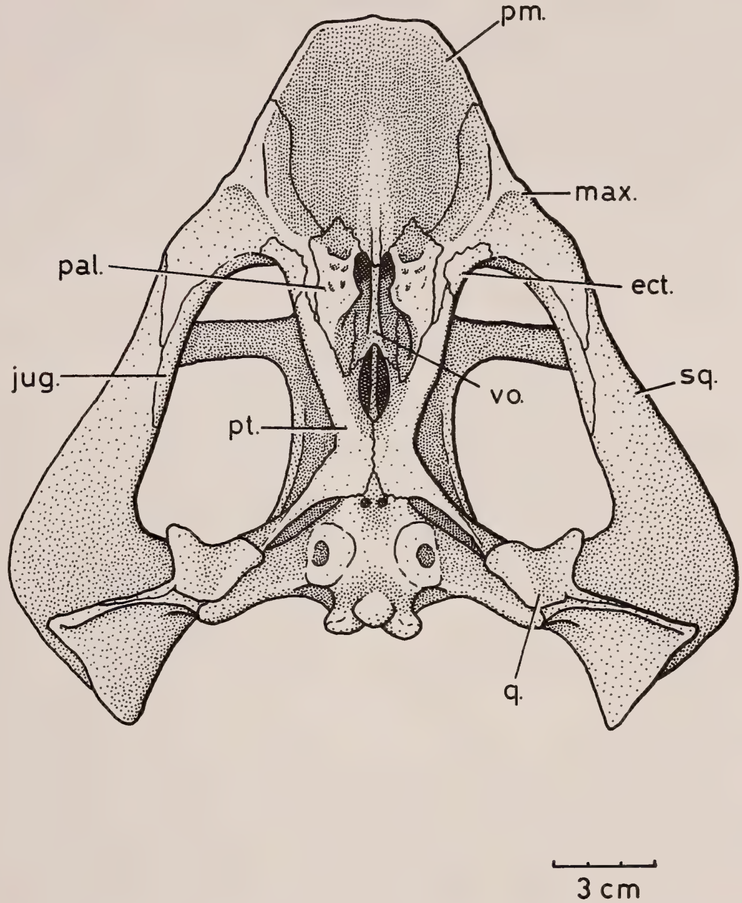

Fig. 22. *Pelanomodon moschops*. Type specimen AMNH 5325. Skull in ventral view.

Medium-sized dicynodonts without tusks. Wide intertemporal and interorbital regions. Snout bent downward on nasals, which are bent downward on rest of skull. Postorbital in intertemporal region steep sided. Ridge across snout between prefrontals. Small prefrontal bosses, larger nasal bosses. No (or reduced) postfrontal bone. No jugal boss. Unbroken palatal rim. Smoothly recessed nostril. Labial fossa present. Relatively short interpterygoidal vacuity. No anterior palatal ridges. Large palatines not bulbous but sloping forward to meet premaxilla. No vomerine trough. Very slight postcaniniform crest.

Related genera

Aulacephalodon and *Pelanomodon* have many features in common, but also some important differences: *Pelanomodon* has a smoothly recessed nostril,

lacks an interpterygoid crest, has a palatine that slopes forward, and lacks anterior palatal ridges, whereas *Aulacephalodon* has a deeply recessed nostril, a palatine with an anterior bulbous portion, anterior palatal ridges, and an interpterygoid crest.

These features and the rarity of *Pelanomodon* specimens relative to *Aulacephalodon* argue against *Pelanomodon's* being merely the female of *Aulacephalodon*, although it is possible that *Pelanomodon* specimens have been misidentified in the past. Both *Dicynodon sidneyi* Broom, 1940, and *D. locusticeps* Huene, 1942, are probably members of *Pelanomodon*, the former being a small member of the genus.

Keyser (1972) considers that the similarities between the two genera are the result of a similar biting mechanism, both forms possibly feeding among vegetation in shallow water.

It is considered here that *Pelanomodon* and *Aulacephalodon* are closely related genera that should be kept separate, at least for the present, until more of the tuskless forms can be investigated.

Genus *Dicynodon* Owen, 1845

Type species *Dicynodon lacerticeps* Owen, 1845

Type material

Skull and lower jaw BMNH 36233.

Locality

Tarka prolongation of the Winterberg, Cape Province.

Stratigraphic horizon

Uncertain.

Diagnosis

The genus *Dicynodon* (Figs 23–26) has recently been revised and illustrated by Cluver & Hotton (1981) and their diagnosis with slight modification will be used here.

Medium-sized to large dicynodonts (average skull length 100 mm to over 400 mm), single pair of maxillary tusks in upper jaw, lower jaw edentulous. Postorbitals tend to cover parietals behind pineal foramen. Septomaxilla merges smoothly with outer surface of snout, does not meet lacrimal. Low boss formed over external nares by nasals. Palatal rim sharp edged, uninterrupted by notch. Palatal portion of palatine large and flat, making short contact with premaxilla. Vomers form long, narrow septum in interpterygoidal fossa. Anterior border of interpterygoidal fossa formed by a crest that joins the vomerine septum. Ectopterygoid small, displaced laterally. Labial fossa present between maxilla, palatine and jugal. Pterygoid makes short contact with maxilla. Basioccipital tubera separated by intertuberal ridge. Fused dentaries carry narrow

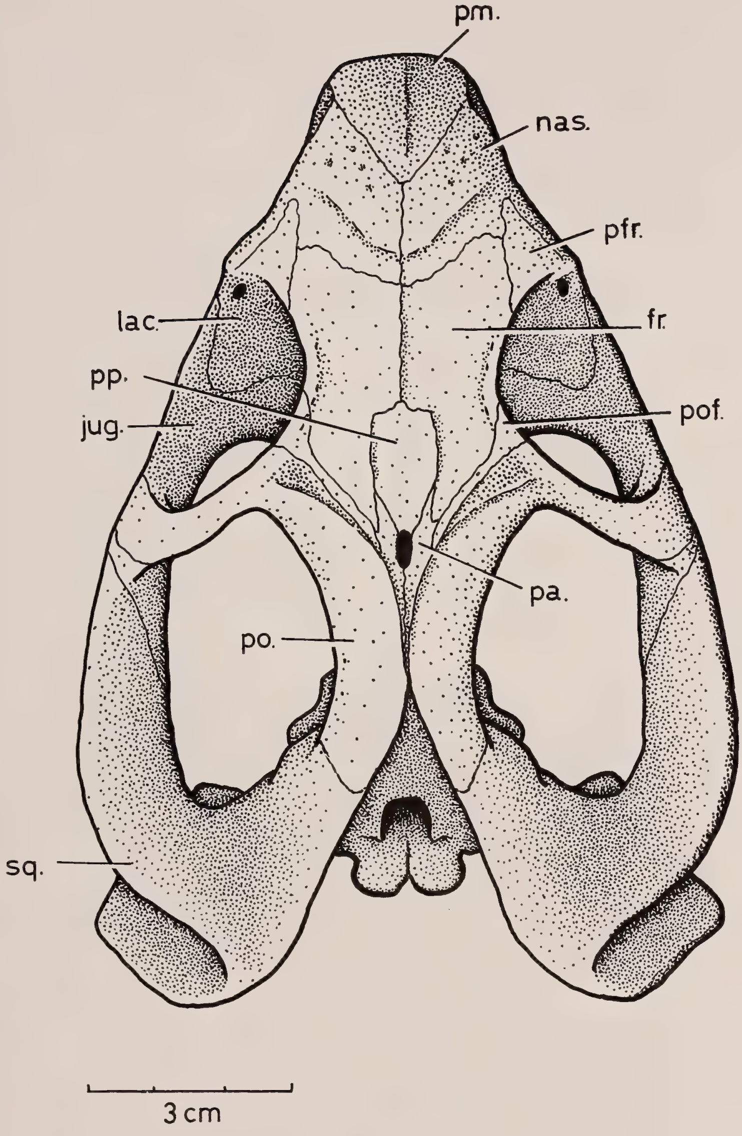

Fig. 23. *Dicynodon* sp. SAM–B88, from Hoeksplaas, Murraysburg. Skull in dorsal view.

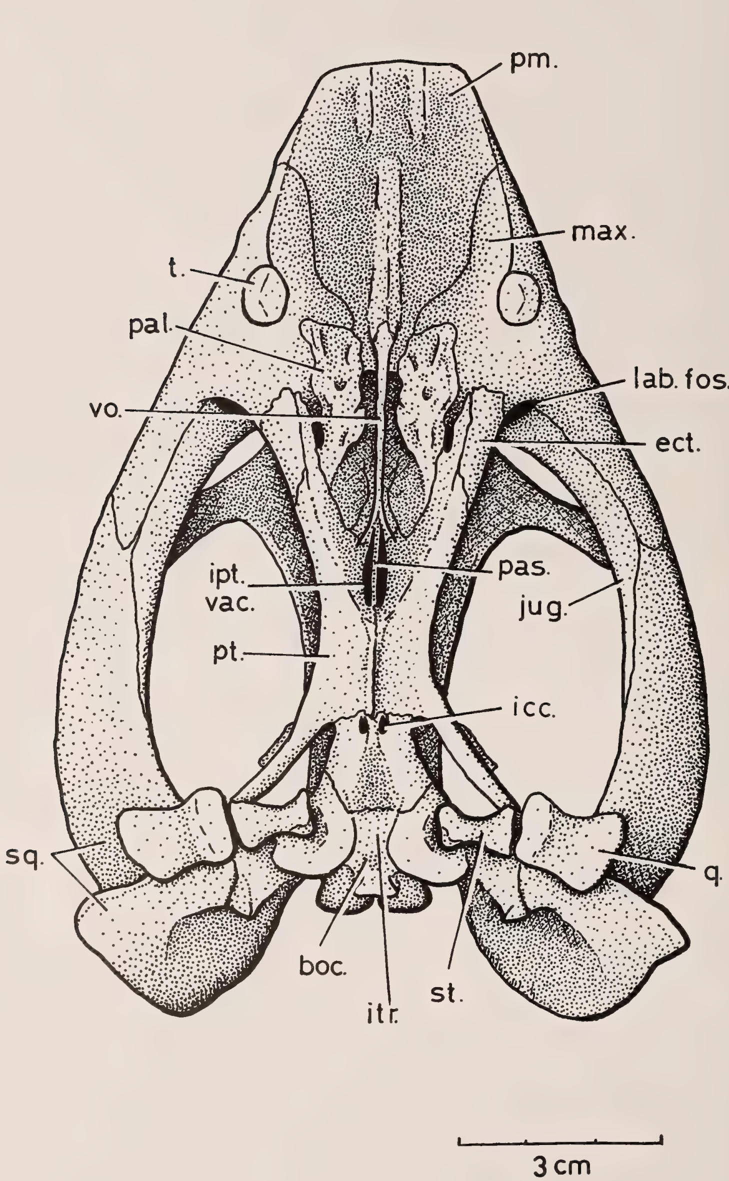

Fig. 24. *Dicynodon* sp. SAM–B88. Skull in ventral view.

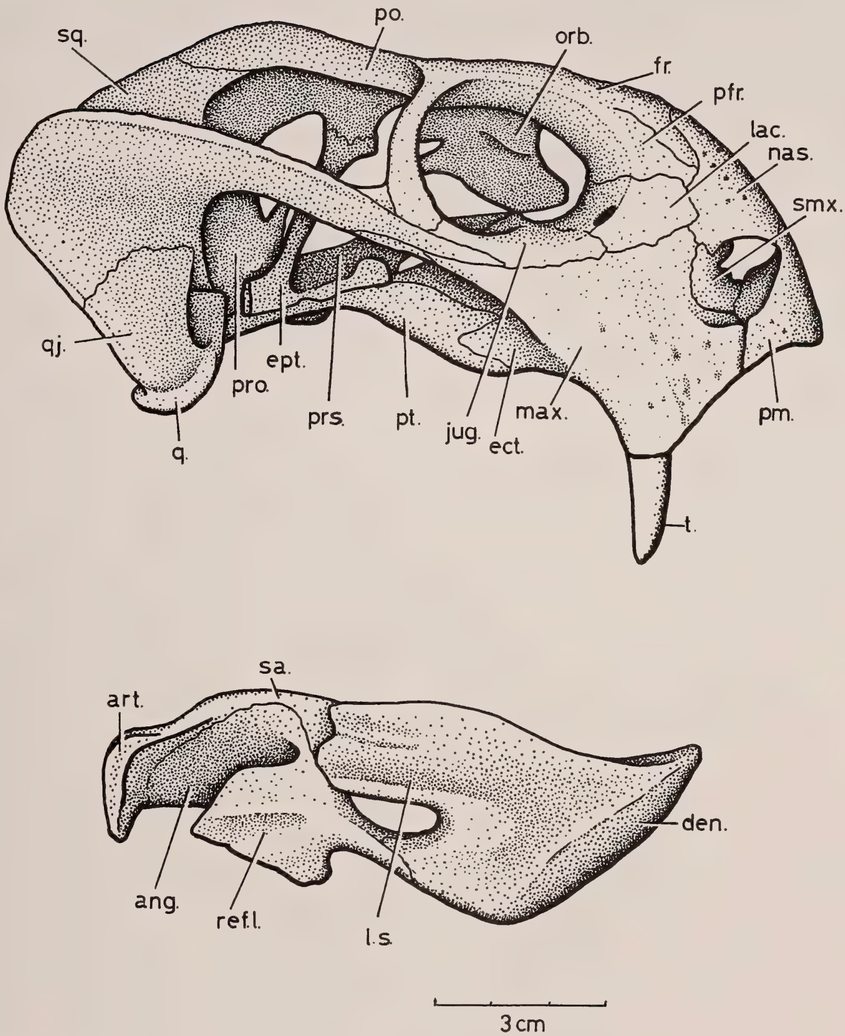

Fig. 25. *Dicynodon* sp. SAM–B88. Skull and lower jaw in lateral view.

dentary tables. Dorsal edge of dentary carries deep sulcus behind dentary tables. Rear of dentary extended dorsally to form weak posterodorsally directed process. Mandibular fenestra large, bounded dorsally by lateral dentary shelf. Occipital surface of opisthotic carries depression above paroccipital process.

Note on the large tusked dicynodonts

Several large tusked dicynodonts have been described in the literature, not only members of the genus *Dicynodon* but also of *Dinanomodon* (Broom 1938) and *Odontocyclops* (Keyser & Cruickshank, 1979). Such forms are characterized by a narrow intertemporal region where the postorbitals overlap the parietals to some degree, absence of a pineal boss, absence of a postcaniniform crest (where it is possible to investigate this feature), and the presence of tusks. In some forms (*Dicynodon njalilus* and *Dinanomodon* spp.) the postorbitals meet over the parietals, obliterating their exposure on the skull roof. In these forms the pineal opening is reduced to a very narrow slit, which does not seem to be the result of lateral compression since the basicranial axis shows no signs of deformation.

It is possible that all these forms are simply large members of a species of *Dicynodon* such as *Dicynodon* (previously *Daptocephalus*) *leoniceps* (Cluver & Hotton 1981). The palatal structure is quite consistent with this. It is possible that the very close overlap of the postorbitals in some forms may be related to large size or advanced age.

The genus *Odontocyclops* was erected by Keyser & Cruickshank (1979) who considered it to be related to *Dicynodon leoniceps* and *Dinanomodon* by the following features that few other Permian dicynodonts share: a small posteriorly placed interpterygoid vacuity with raised margins, an anterior process of the footplate of the epipterygoid, a large posterior extension of the premaxilla in the secondary palate, reduction of the ectopterygoid, a high position in the snout of the external nostril, contact between the maxilla and septomaxilla, the small pineal foramen, and absence of a pineal boss.

In fact, most of these features are widespread in the genus *Dicynodon* and do not serve to

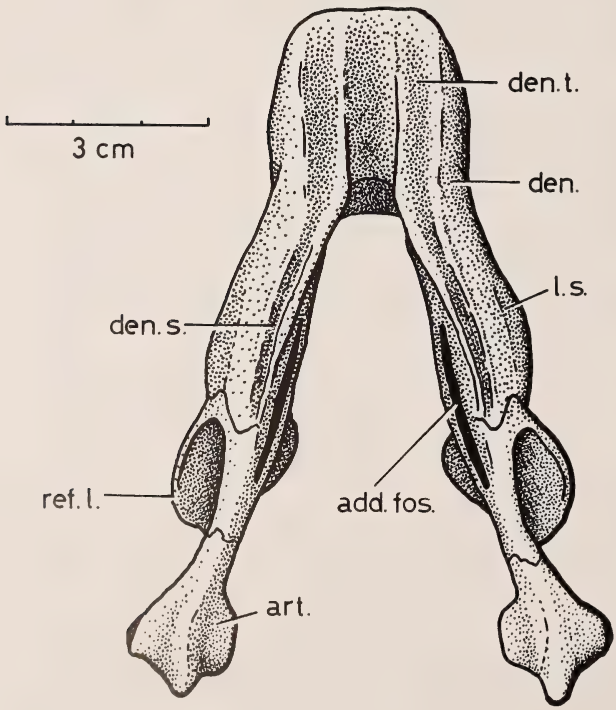

Fig. 26. *Dicynodon* sp. SAM–B88. Lower jaw in dorsal view.

separate the three forms mentioned above from other members of that genus. For example, *Dicynodon* sp. SAM–B88 (Cluver & Hotton 1981) shows all the above features.

The anterior process of the footplate of the epipterygoid is not a feature that is particularly useful for taxonomic purposes since the ossification of this process is very variable; however, judging from the groove present on the lateral surface of the pterygoids, an extension of the footplate was present in most Permian forms (including *Eodicynodon*) whether cartilaginous or bony.

Keyser & Cruickshank (1979) distinguish *Odontocyclops* from the other two related genera, *Daptocephalus* (i.e. *Dicynodon leoniceps* of our classification) and *Dinanomodon* on the following features: the concavity of the dorsal snout surface, the broad intertemporal region, and large size. These features are used to demonstrate that *Odontocyclops* cannot be ancestral to the long-snouted Triassic forms with a crested intertemporal and, while this may be so, nevertheless there is nothing in this character suite that debars *Odontocyclops* from the genus *Dicynodon*. The intertemporal region mentioned is broad relative to the Triassic forms, but it is not outside the range of variation tolerable within the genus *Dicynodon* and is shown by species such as *D. calverleyi* and *D. bathyrhynchus*.

In conclusion, it is proposed that large tusked forms such as *Odontocyclops* and *Dinanomodon* be accommodated within the genus *Dicynodon*, as they probably represent large members of a species such as *D. leoniceps* or are distinct but closely related species.

Genus *Robertia* Boonstra, 1948

Type species *Robertia broomiana* Boonstra, 1948

Type material

Skull SAM–11761.

Locality

Klein Koedoeskop, Beaufort West, Cape Province.

Stratigraphic horizon

Tapinocephalus Zone.

Remarks on the type specimen

The genus is represented only by *Robertia broomiana*. The type specimen consists of most of a skull and lower jaw reasonably well preserved but embedded in an intractable matrix. Little preparation has been carried out.

The original description (Boonstra 1948) includes the following features: the skull is relatively broad with a maximum length of 80 to 100 mm; the snout is weak and short; the small nostril opens near the alveolar border; the interorbital width is less than the intertemporal width; the molar teeth are small, simple cones arranged in the lower jaw in a single fairly regular row along the lingual side of the dentary; the dentary teeth are 5 to 9 in number; and the upper postcanine teeth all lie on the maxilla posterolingual to the canine or caniniform process, forming an irregular group of one to eight.

The original description is based on several topotypes and referred specimens as well as the type specimen.

Toerien (1953) added a figure and described another specimen assigned to *Robertia broomiana*. He noted that the anterior ramus of the pterygoid bears a ridge continuous with the alveolar border.

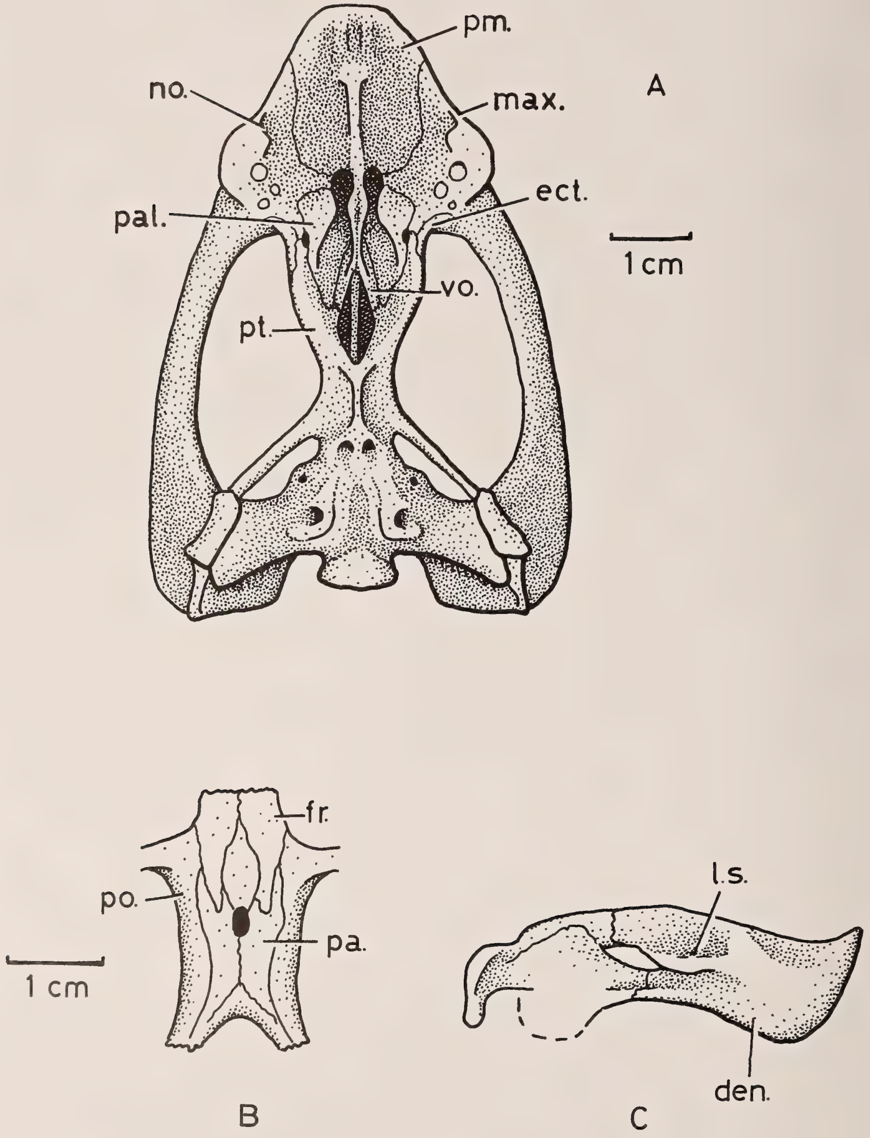

Fig. 27. A. *Robertia* sp. SAM–11461, from Buffelsvlei, Prince Albert. Skull in ventral view. B–C. *Robertia* sp. SAM–11885, from Michau's Request, Beaufort West. Skull roof and lower jaw.

Description of additional specimens

The following description is based on material in the South African Museum that can be assigned to the genus *Robertia* according to the description above. The specimens are SAM–11885 (Fig. 27B–C) from Michau's Request, Beaufort West, SAM–11890 from Skoorsteen, Laingsburg, SAM–K296 (Fig. 27A) from Die Krans van Tuinkraal, Beaufort West, and SAM–11451 from Buffelsvlei, Prince Albert.

A full description of *Robertia* does not exist at present in the literature, so a rather more detailed description than for other specimens is given here.

Skull length ranges between 60 and 100 mm. Tusks may or may not be present. The intertemporal and interorbital widths are approximately equal. The parietals are exposed behind the pineal foramen giving a moderately wide intertemporal region. The preorbital widths are approximately equal. The preorbital region is shorter than the length of the orbit. Unlike species of *Emydops* or *Pristerodon*, the maxillary rim is drawn down round the tusk or into the caniniform process.

A few (usually three) postcanine teeth are present on the maxilla in a more or less straight line posteromedial to the canine or caniniform process. Anterior to the canine or caniniform process there is a notch in the maxilla, which cuts back into the medial surface of the caniniform process or into the bone sheathing the tusk.

The palatine is of moderate size. It forms part of the surface of the secondary palate and is continuous horizontally with the premaxilla. The palatine approaches the vomer but does not make contact with it. Posterior to the level of the palatines, the ventral edge of the median plate of the vomers runs posterodorsally and bears a wide trough. The sides of the trough separate posteriorly to form the anterior border of the interpterygoid vacuity. A short median palatal ridge is present anteriorly where the median vomer plate meets the premaxilla.

The anterior rami of the pterygoids are strong. Posteriorly each ramus bears a high, sharp ridge. The ridges converge towards the midline where they fuse together and continue posteriorly as a single median ridge, which runs in the midline of the posterior part of the pterygoid and over the basisphenoid. A Y-shaped system of ridges therefore dominates the pterygoid-basisphenoid area of the palate.

The interpterygoid vacuity is moderately extensive. Its length is half that of the distance between its posterior edge and the anterior border of the choana.

The foramina for the passage of the internal carotid arteries are prominent. They are situated immediately behind the median pterygoid-basisphenoid ridge and face ventrally.

The quadrate bears a shallowly convex medial and lateral condyle. The lateral condyle is marginally the greater in area. The lower jaw is fairly robust with a sharp, squarish tip. Anteriorly it bears well-defined dentary tables on the

dorsal surface. A longitudinal dentary sulcus is not present on the dorsal surface of the jaw ramus.

A few small teeth are present on the dentary.

The lateral surface of the dentary is built up into a ledge approximately one-third of the length of the jaw. The ledge is directed ventrally so that its outer surface faces mostly laterally and so tends to occlude the mandibular fenestra. There are marked striations on the lateral surface of the dentary ledge.

The posterior part of the jaw is typically dicynodontian with a downwardly projecting retroarticular process and an elongate lateral articular condyle.

Diagnosis

Taking into account the new material, the following generic diagnosis may be formulated.

Small to medium (up to 12 cm skull length) dicynodonts. Intertemporal region moderately wide and parietals exposed. Tusks present or absent. Maxillary rim extended ventrally round tusk or into caniniform process. Approximately three postcanine teeth arranged in a row in the maxilla. Notch present on the palatal surface of the maxilla. Palatine moderately large but does not reach the vomers. Y-shaped ridge dominates the pterygoids and basisphenoid. Trough on the ventral edge of the median plate of vomer. Dentary tables on lower jaw. A few small teeth present on the dentary. A lateral dentary shelf takes up the middle third of the length of the jaw and is directed ventrally so that it tends to occlude the mandibular fenestra.

Genera *Brachyuraniscus* Broili & Schröder, 1935
and *Brachyprosopus* Olson, 1937

The taxonomic status of the following genera from the *Tapinocephalus* Zone of the Beaufort Group is enigmatic.

Brachyuraniscus reuningi was described by Broili & Schröder (1935) and two new species were added to the genus by Toerien (1953). The new species were *B. merwevillensis* and *B. broomi*, the latter a redesignation of *Brachyprosopus broomi* (Olson 1937). Toerien considered that *Brachyprosopus broomi* was so similar to *Brachyuraniscus* in palatal features that it should be included in the same genus. However, he overlooked the very different shape of the palatine in *Brachyprosopus* and the fact that this form apparently has a labial fossa.

The type specimens of both *Brachyuraniscus merwevillensis* and *reuningi* have been lost. The figures of *Brachyuraniscus merwevillensis* (Toerien 1953) do not allow much detail to be discerned, and those of *B. reuningi* show it to be a very incomplete specimen. It is felt, therefore, that no useful purpose is served in trying to establish the relationships of these two forms. It would seem, however, that *Brachyprosopus* is a distinct genus. It shows certain primitive features such as the short secondary palate, a number of well-

developed postcanine teeth, the wide intertemporal region with the parietals exposed, and features of the braincase, which Olson (1937) described. The presence of a labial fossa and the shape of the palatine in not encroaching upon the midline seem to be distinctive features. Even so, without further information, especially from the lower jaw, it is difficult to define the relationships of *Brachyprosopus* very accurately, and it is at present left *incertae sedis* as there is insufficient evidence to determine its taxonomic position.

Genus *Diictodon* Broom, 1913

Diagnosis

This genus has recently been reviewed by Cluver & Hotton (1981) and their diagnosis with minor modifications will be used here. (See Figs 28–30.)

Medium-sized dicynodonts (average skull length 110 mm), jaws either lacking teeth altogether or bearing a single pair of maxillary tusks. Postorbitals tend to cover parietals behind pineal foramen. Septomaxilla recessed within external naris, maxilla rises high on the side of the snout to meet nasal. Nasal forms boss over external naris. Maxilla carries a prominent caniniform process clearly demarcated from anterior palatal rim by a deep notch. Palatal portion of palatine small, does not meet premaxilla. Vomers form short septum in interpterygoid fossa. Ectopterygoid large, separating pterygoid from maxilla. Fused dentaries carry wide dorsal dentary tables, with high medial borders. Rear of dentary table extended medial to level of inner surface of jaw ramus. Dorsal edge of dentary rounded behind dentary table, no posterior dorsal process of the dentary present. Mandibular fenestra large, no expanded lateral dentary shelf for insertion of adductor musculature.

Genus *Emydops* Broom, 1912

Type species *Emydops minor* Broom, 1912

Type material

Skull and lower jaw AMNH 5525.

Locality

Kuilspoort, Beaufort West, Cape Province.

Stratigraphic horizon

Cistecephalus Zone.

Remarks on the type specimen

The skull and jaw are obliquely crushed and the snout badly damaged (Fig. 31C). The skull roof behind the snout region is exposed and sutures can be distinguished. Teeth are not visible although Broom (1913) stated that, having broken the specimen through, he could see ‘at least two small teeth’. When

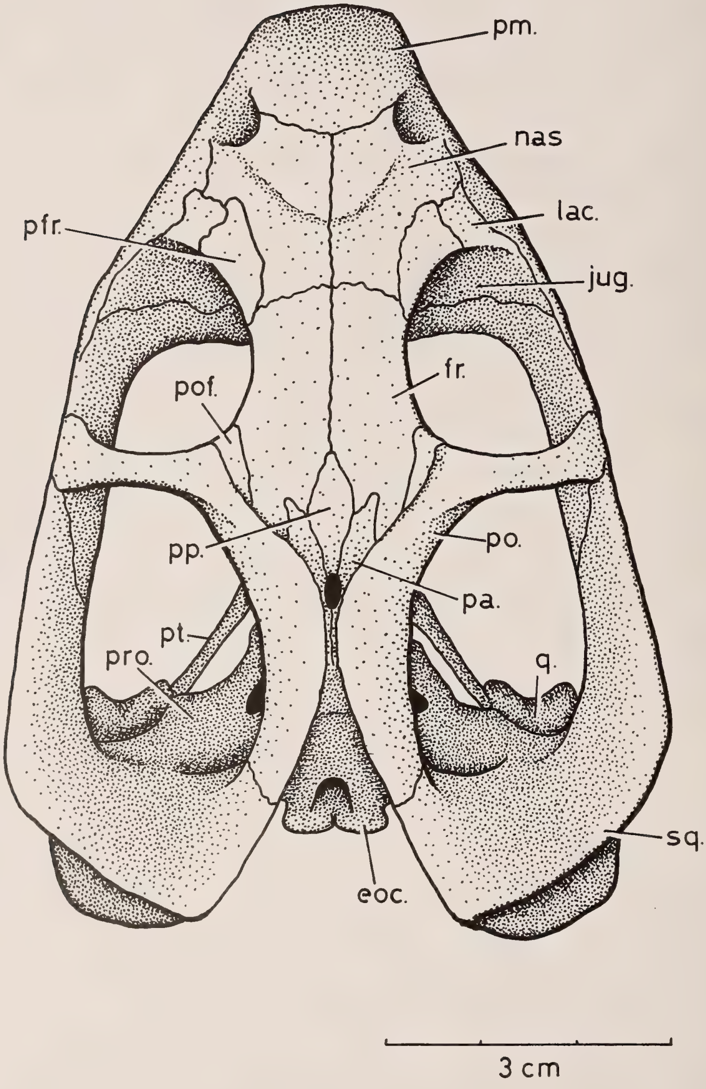

Fig. 28. *Diictodon* sp. SAM–10086, from Dunedin, Beaufort West. Skull in dorsal view.

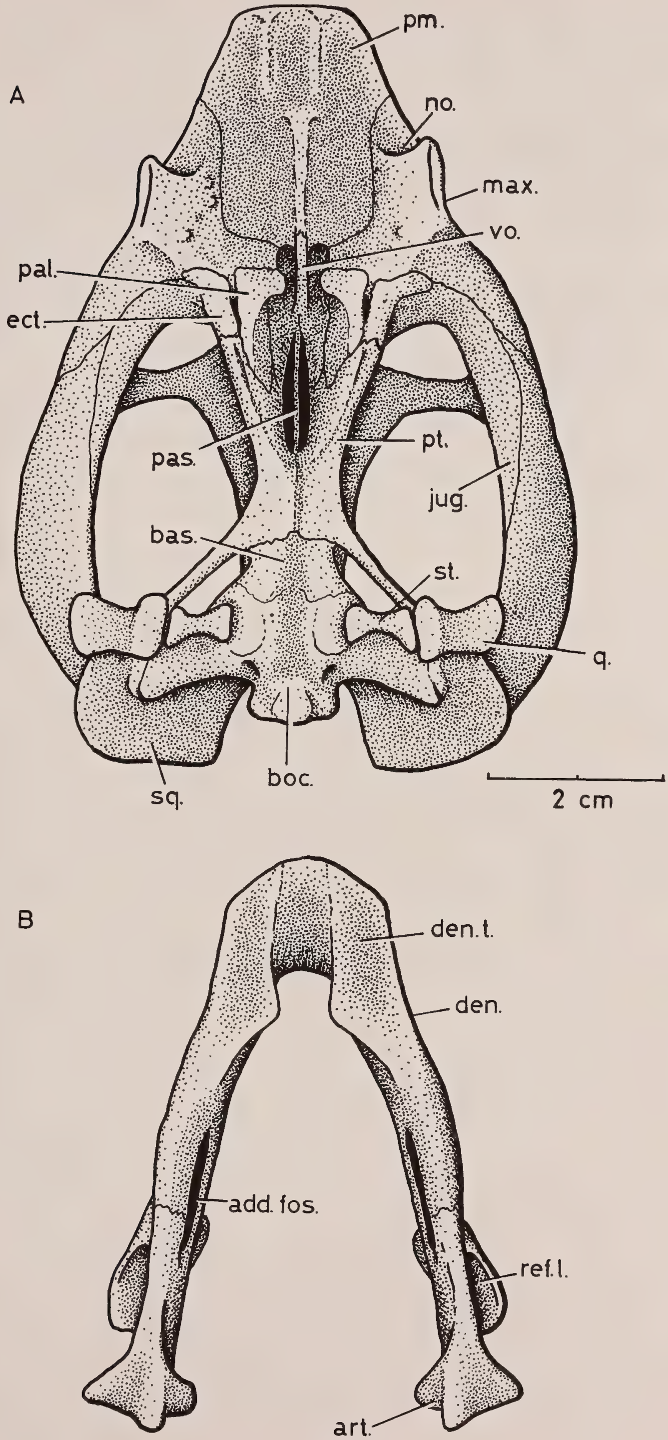

Fig. 29. *Diictodon* sp. SAM–10086. A. Skull in ventral view. B. Lower jaw in dorsal view.

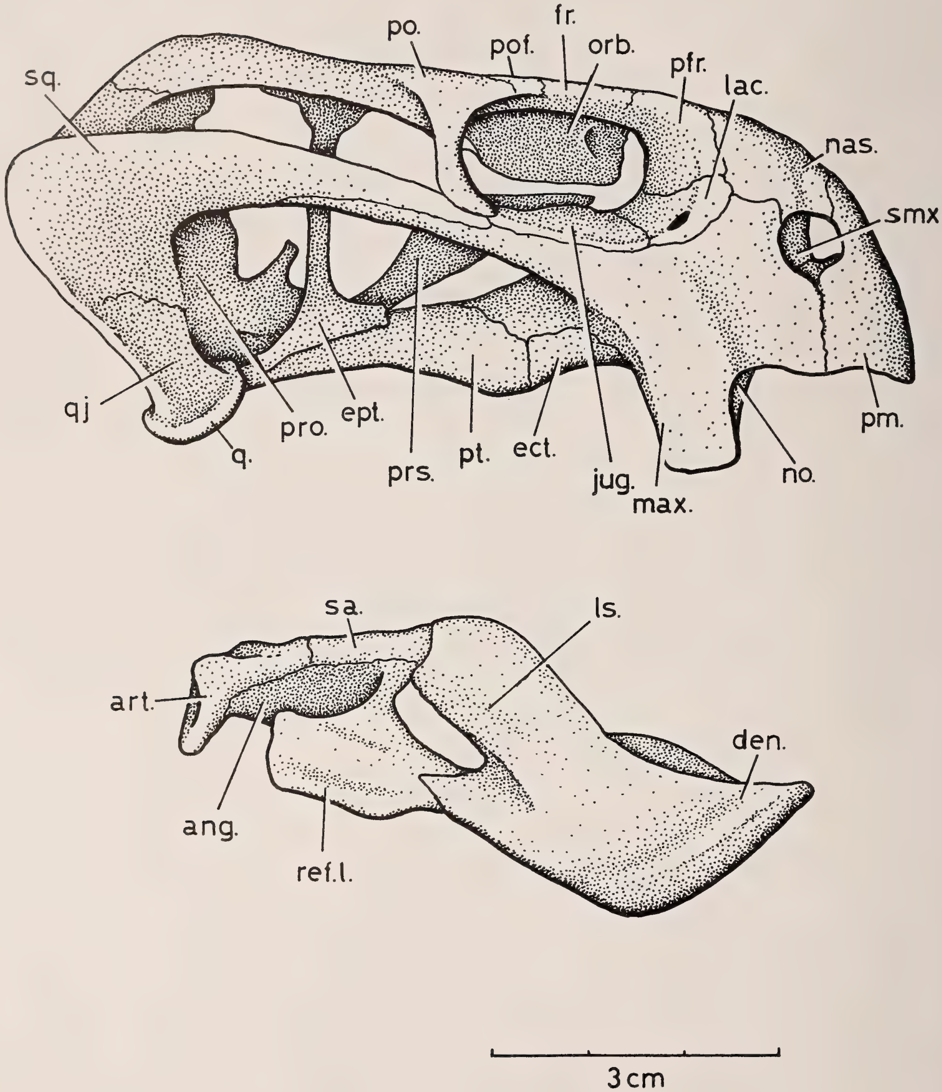

Fig. 30. *Diictodon* sp. SAM–10086. Skull and lower jaw in lateral view.

examined by M.A.C. in 1973 the anterior part of the snout was in a delicate state of preservation and it was thought unwise to loosen the several pieces of bone and matrix to verify Broom's observation.

On the skull roof the parietals are widely exposed between the postorbitals and a short wedge-shaped postfrontal is present. The palate is totally obscured and would require extensive preparation for detail to be revealed.

The lower jaw is preserved *in situ*, but few details can be made out. The symphysial region appears relatively weak.

Although this specimen is that on which Broom based the genus *Emydops*, regrettably few characters of taxonomic importance are visible. However, the name *Emydops* is now well entrenched in the literature and has become accepted as indicative of a taxon with characters that are seen in type specimens of other species currently assigned to *Emydops*. As in the case of *Pristerodon*, it is suggested here that in the interests of nomenclatural stability the name *Emydops* should be retained and the characters seen in secondary type material be included in the overall generic diagnosis.

Other Emydops species

The description of *Emydops longiceps* by Broom (1913) was based on a skull from Lemoenfontein, Beaufort West (AMNH 5578). The specimen is a weathered skull lacking lower jaw and with the occiput incomplete. The relationships between parietals, postfrontals, and frontals are easily seen. In the palate the pterygoids and palatines are crushed and broken but it is possible to provide a reasonable reconstruction. The palatal portion of the palatine is quite large and extends forward to meet the premaxilla. The vomer, which is excavated ventrally in the form of a longitudinal trough, meets the posterior tip of the median premaxillary ridge. A single small tooth is present on the maxilla close to the alveolar border. Anterior premaxillary palatal ridges are apparently absent.

Emydops platyceps (Broom & Haughton 1917) is based on a skull from Dunedin, Beaufort West (SAM–2667). The skull roof is complete up to the anterior third of the orbit and the relationships between the bones are essentially the same as in the previously described specimen. In the palate each maxilla bears a tusk, and there are two small postcanine teeth posteriorly on the left-hand side. The palatal portion of the palatine is quite large but broken by a notch in its medial border. The palatine reaches forward to the level of the rear of the premaxilla. Anterior premaxillary ridges are absent but a pair of longitudinal grooves runs alongside the median palatal ridge to the level of the canine tusk. The rear of the vomerine septum is trough-shaped but the more anterior part is thin and blade-like.

The description of *Emydops longus* (Fig. 31A–B) by Broom (1921) was based on a skull and lower jaw from Biesjiespoort, Victoria West (BMNH R4956). The skull is dorsoventrally crushed and the snout damaged by an early attempt at preparation. On the skull roof the parietals are very widely exposed.

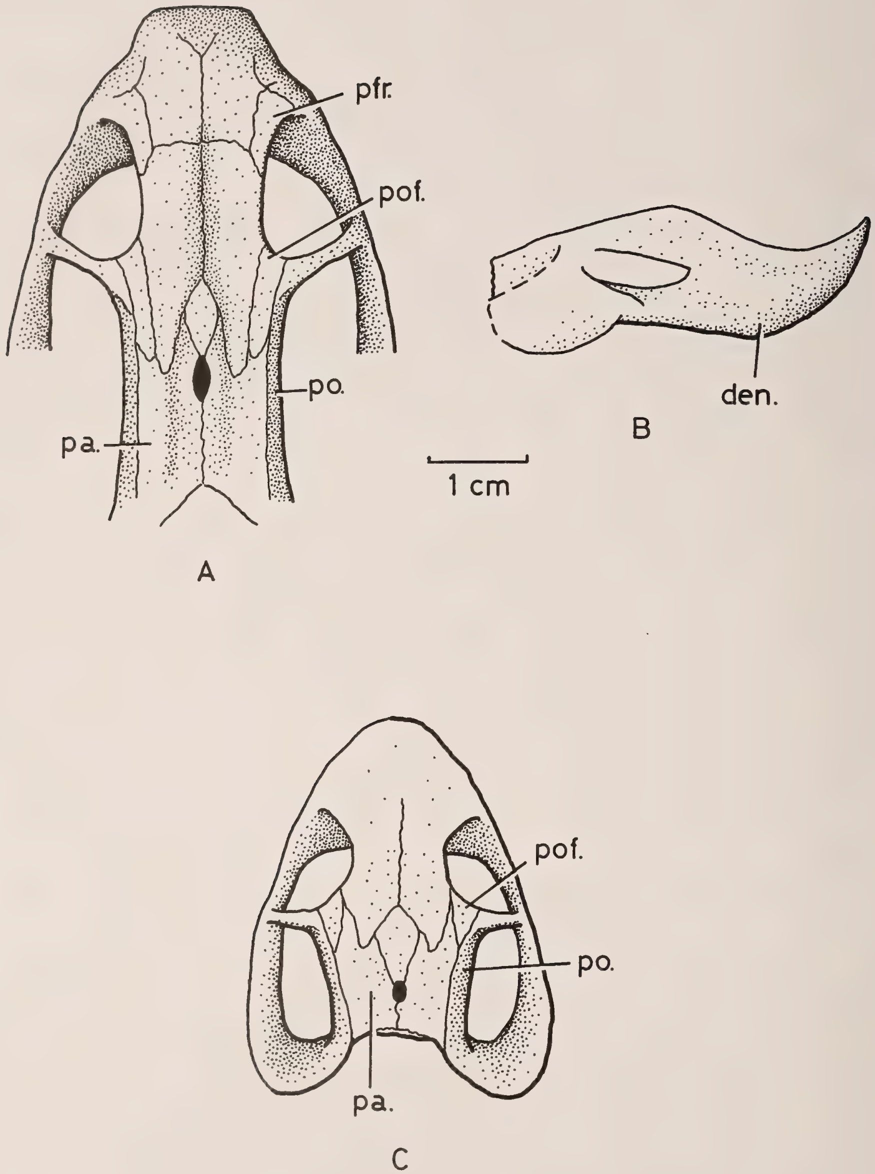

Fig. 31. A–B. *Emydops longus*. Type specimen BMNH R4956, from Biesjiespoort, Beaufort West. A. Skull in dorsal view. B. Lower jaw in lateral view. C. *Emydops minor*. Type specimen AMNH 5525, from Kuilspoort, Beaufort West. Skull in dorsal view.

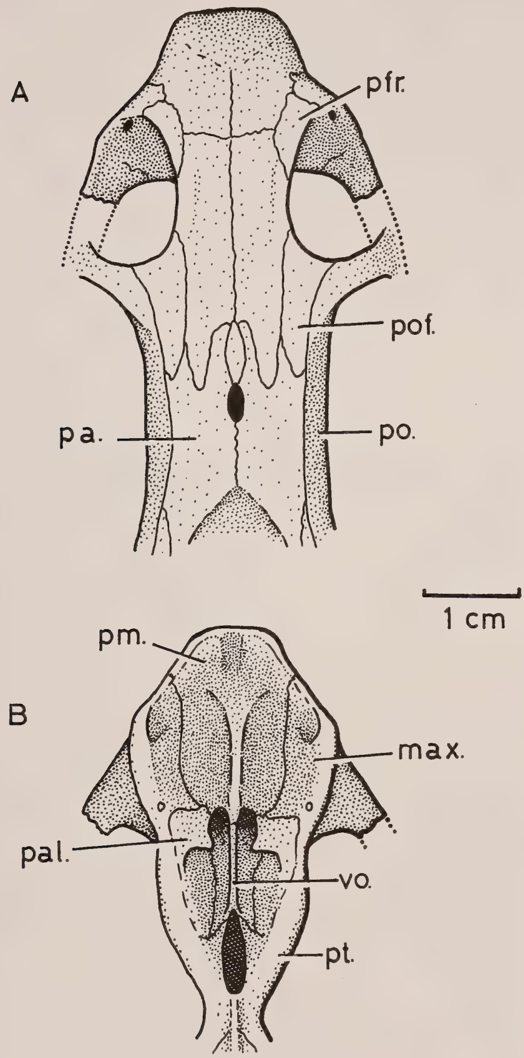

Fig. 32. *Emydops longus*. Paratype BMNH R4957, from Biesjiespoort, Victoria West. A–B. Skull in dorsal and ventral views.

The postorbitals lie along the side of the intertemporal bar, forming the medial borders of the temporal fenestra.

The palate is obscured by the lower jaw but a single tooth is visible close to the alveolar border behind the caniniform process.

The lower jaw has a prominent lateral dentary shelf and a sharp shovel-shaped symphysis. At least four teeth are present on the dorsomedial edge of the dentary. One of the teeth shows a distinct row of five posterior serrations. Because of damage during earlier preparation part of the dentary is lost and a complete tooth count is not possible.

The paratype of *Emydops longus*, (BMNH R4957, Fig. 32) adds considerable information concerning the morphology of the species. The postorbital lies on the side of the intertemporal bar, as in the type specimen, and has

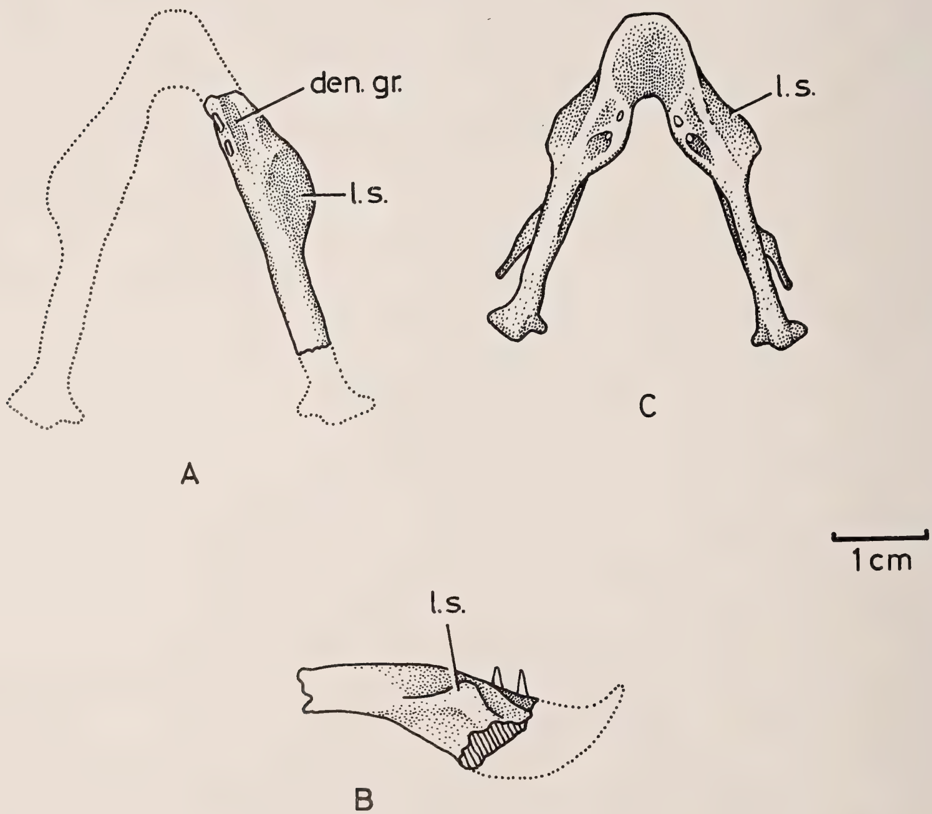

Fig. 33. A–B. *Emydops brachyops*. Type specimen SAM–708 from 'The Gouph', Beaufort West. Right ramus of lower jaw in dorsal and lateral views. C. *Emydops* sp. SAM–10172, from Dunedin, Beaufort West. Lower jaw in dorsal view.

practically no dorsal skull roof exposure. The maxilla rises fairly high on the side of the snout and confines the lacrimal to the anterior border of the orbit.

In ventral view the vomer is seen to border only the anterior part of the interpterygoidal vacuity, but does not form a trough-like anterior extension of the vacuity. The palatal portion of the palatine is a horizontal plate transversely extended to form a posterior extension of the premaxillary secondary palate, making a brief contact with the premaxilla. The posterior border of the palatal portion is concave. The palatal rim is interrupted at the level of the caniniform process and a medial embayment is formed anterior to the weak caniniform

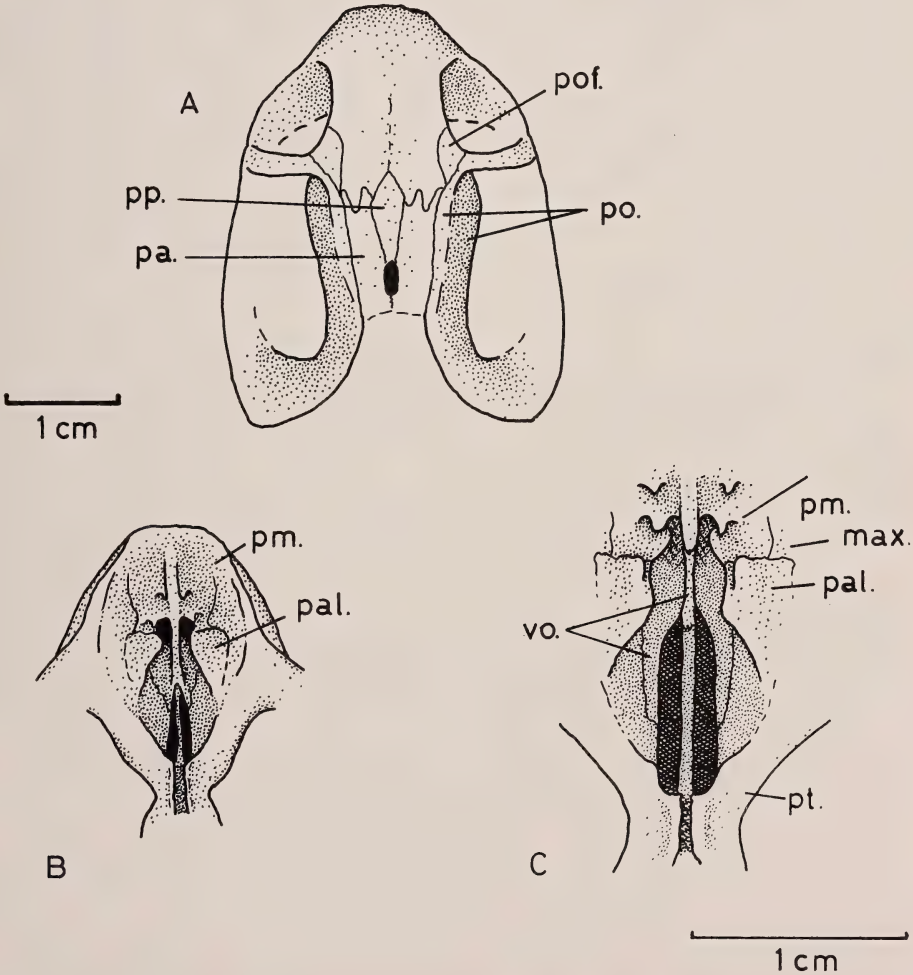

Fig. 34. *Emydops parvus*. Type specimen BMNH R4960, from Bruintjieshoogte, Somerset East. A–B. Skull in dorsal and ventral views. C. Detailed palatal view.

process. A raised ledge is formed medial to the caniniform process. A single small tooth lies behind the process, close to the alveolar border.

The lower jaws in the type specimen of *Emydops brachyops* (Broom), SAM–708 (Fig. 33A–B), and in SAM–10172 (Fig. 33C) indicate that a short, shallow groove extends back along the dorsal edge of the dentary behind the symphysial region.

Diagnosis

Taking into account the information gained from the various species of *Emydops* described above (see also Figs 34–35), it is possible to formulate the following generic diagnosis.

Small dicynodonts with broad intertemporal region and wide parietal exposure on the skull roof. Palatine meets posterior border of premaxilla and is transversely enlarged into a horizontal plate with a concave posterior border. Anterior trough-like extension of the interpterygoidal vacuity on to the vomerine septum short or absent. Embayment in palatal rim anterior to caniniform process. Interpterygoidal crest weak, not continued on to ventral surface of anterior pterygoid ramus. Dentary shelf prominent. Anterior symphysial region of dentary drawn up into a sharp cutting edge. Shallow groove on dorsal edge of dentary behind symphysis.

Related genera

Cluver (1974*b*) has discussed the possible relationships of *Emydops*, *Myosaurus*, *Myosauroides* and *Cistecephalus*. His conclusion that the last three genera are probably quite closely related and may have arisen from an *Emydops*-like ancestor, is accepted here.

Genus *Kingoria* Cox, 1959

Diagnosis

This genus (Figs 36–38) has recently been reviewed by Cluver & Hotton (1981). Their diagnosis with minor modifications will be used here.

Medium-sized dicynodonts (average skull length 160 mm), jaws lacking teeth altogether or bearing a single pair of maxillary tusks. Parietals exposed between postorbitals behind pineal foramen. Septomaxilla recessed within opening of naris, maxilla rises high on the side of the snout to meet nasal. Low boss formed by nasal. Maxilla carries prominent caniniform process. Rear of caniniform process extended as a keel to level of ectopterygoid. Palatal rim continued without interruption on to anterior blade of caniniform process. Palatal portion of palatine very small, restricted to border of choanal depression but making contact with greatly expanded premaxilla. Vomers form short septum in interpterygoidal fossa. Ectopterygoid large, separating pterygoid from maxilla. Fused dentaries taper to form rounded anterior tip of lower jaw, no dentary tables present. Dorsal edge of dentary narrow, lateral dentary shelf

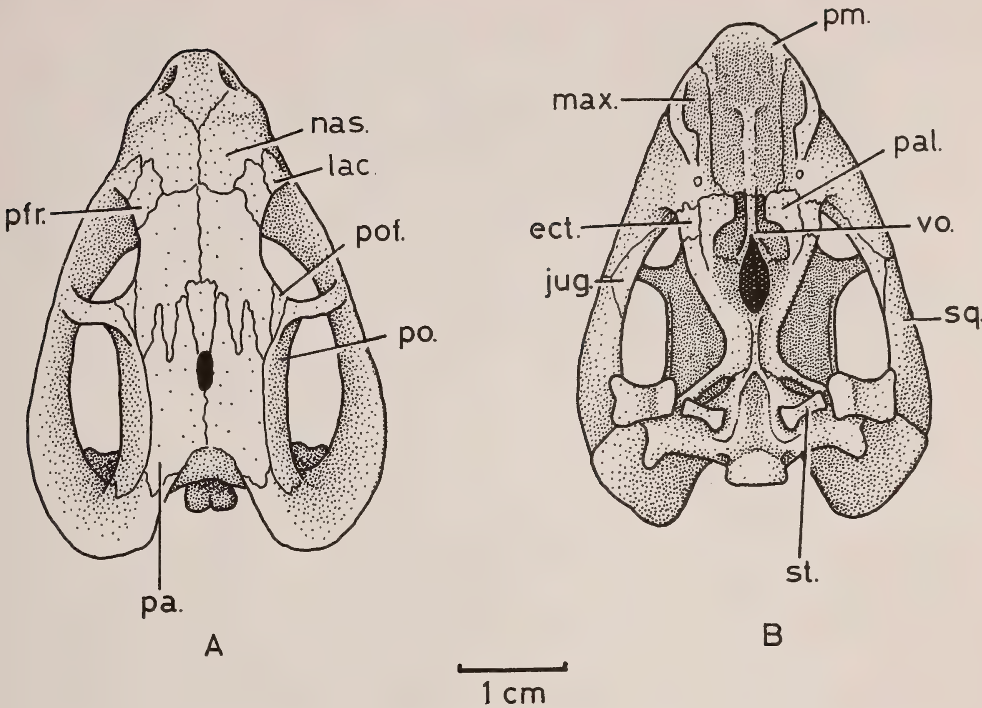

Fig. 35. *Emydops* sp. SAM–11060, from Leeuwkloof, Beaufort West. A–B. Skull in dorsal and ventral views.

widely expanded. Mandibular fenestra reduced or absent. Angular forms sharp ventral keel behind reflected lamina.

Related genera

The Lower Triassic genus *Kombuisia* (Hotton 1974) may be related to *Kingoria*. Features such as the very small contribution of the palatine to the secondary palate, the large ectopterygoid separating maxilla and pterygoid, the prominent lateral dentary shelf, and absence of the postfrontal may ally the two genera. *Kombuisia* has several specialized characters of its own, and Hotton (1974) discussed possible relationships between these two genera.

PHYLOGENETIC ANALYSIS OF RELATIONSHIPS BETWEEN PERMIAN DICYNODONT GENERA

Introduction

Having established generic diagnoses of several Permian dicynodont genera, an attempt to draw up a scheme of the relationships between these genera may be made. Not all the characters used in the generic diagnoses prove to be

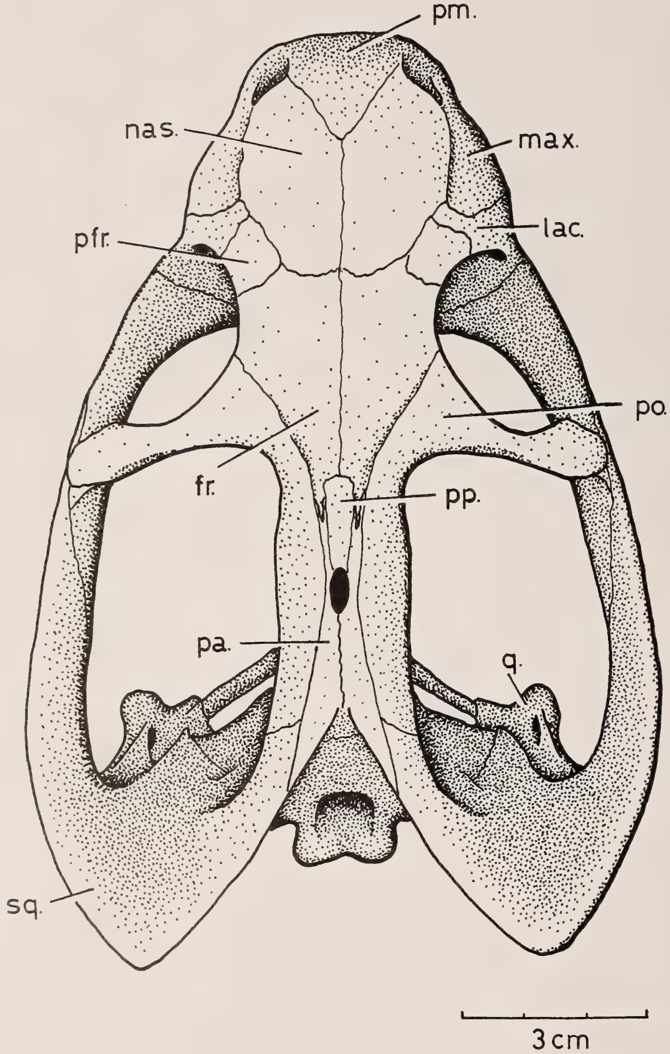

Fig. 36. *Kingoria nowacki*. Skull in dorsal view. (After Cox 1959.)

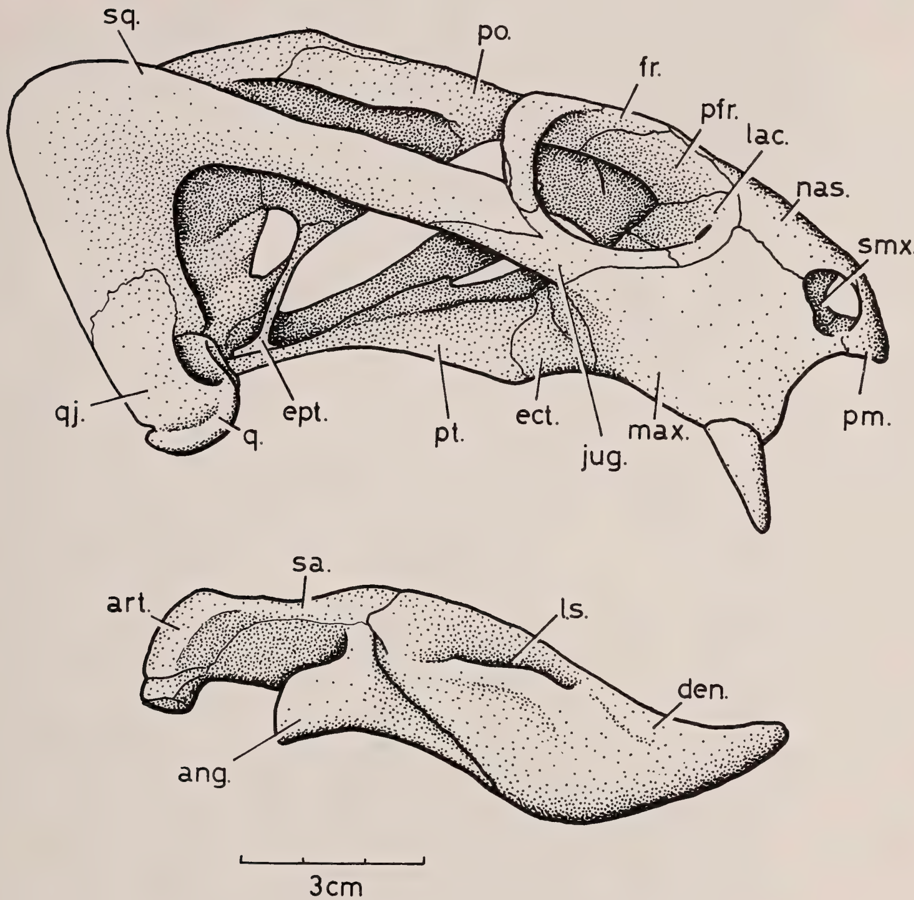

Fig. 37. *Kingoria nowacki*. Skull and lower jaw in lateral view. (After Cox 1959.)

useful in constructing a phylogeny. The characters that are useful are shown below in the character suites. Shared derived characters, where these can be determined, have been used to link related groups. The primitive condition for dicynodonts is taken to be represented most closely by *Venjukovia* (Efremov 1940).

Venjukovia is from Zone II of the Upper Permian of Russia and has been implicated in the evolution of dicynodonts by several workers (Watson 1948; Olson 1962; Tchudinov 1965; Barghusen 1976).

Venjukovia (Fig. 39) exhibits several features that are primitive for therapsids: the premaxillae are paired, the anterior dentition is present, the interptery-

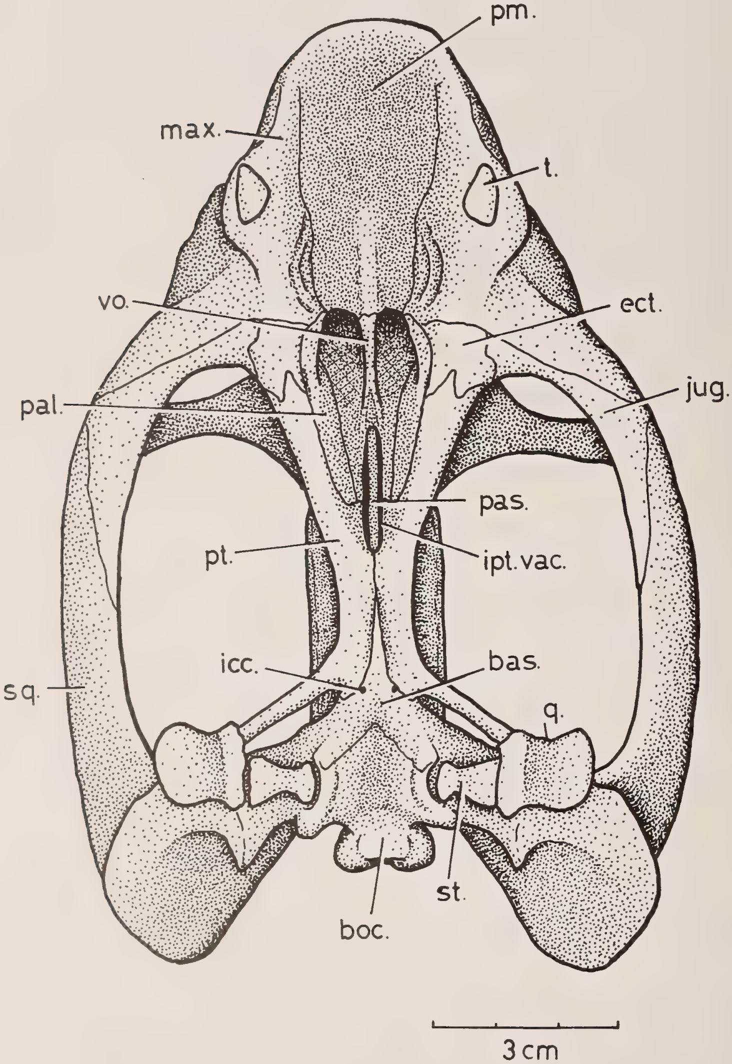

Fig. 38. *Kingoria nowacki*. Skull in ventral view. (After Cox 1959.)

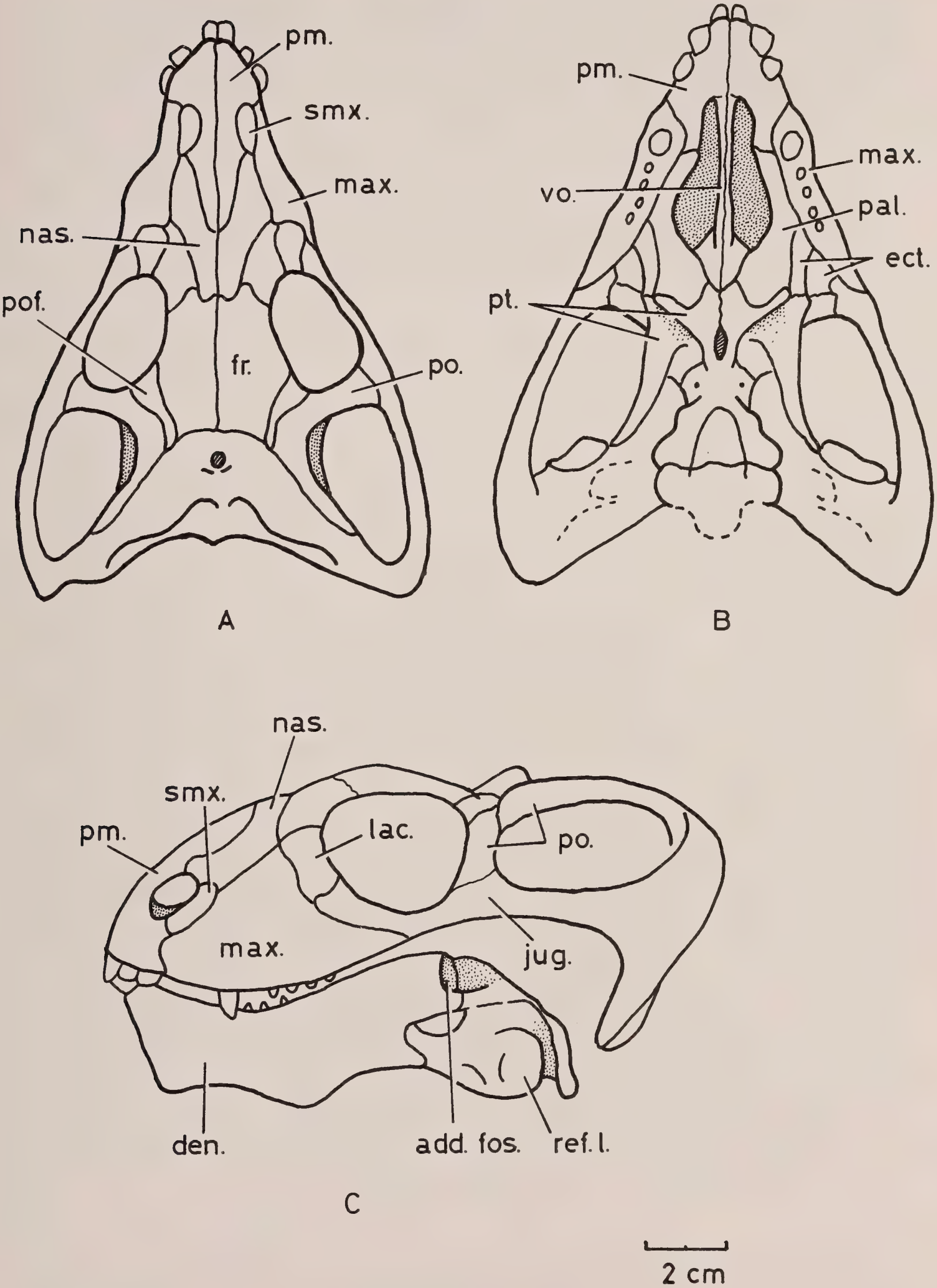

Fig. 39. *Venjukovia* sp. A–B. Skull in dorsal and ventral views. C. Skull and lower jaw in lateral view. (After Barghusen 1976.)

goidal vacuity lies wholly between the pterygoids, the adductor musculature does not extend far forward on the lower jaw, the secondary palate is not extensive compared with later dicynodonts, the lateral pterygoid process (transverse flange) is pronounced, the ventral edge of the median vomer plate bears a shallow trough, and there is no preparietal.

However, *Venjukovia* also exhibits derived characters that ally it with later dicynodonts: the coronoid bone is absent, the preorbital region is short, the lateral pterygoid process is modified and directed anteriorly, the zygoma is emarginated ventrally, musculature attaches to the external surface of the zygoma and to the external surface of the dentary posteriorly, the lower jaw articulation is modified, possibly permitting a sliding action, there is an incipient secondary palate with the palatine beginning to assume a role forming a partial floor to the internal nares as it extends forward and slightly medially, a mandibular fenestra is present, and palatal teeth are lost.

Some of these features may be adaptations for herbivorous feeding, for example the short preorbital region, the reduction and modification of the lateral pterygoid flange, and the low blunt teeth, and there is therefore the possibility that they have evolved in parallel in *Venjukovia* and dicynodonts. However, it is felt that in view of the number of derived characters linking them, it is more parsimonious to assume that the two groups are related. As stated at page 197, the derived character suite given above is taken to define the Dicynodontia, and *Venjukovia* is therefore considered to be a dicynodont.

Venjukovia is here taken to represent an initial stage in the evolution of the later dicynodont groups, and is used for comparison with these later forms that express more fully the dicynodont characters outlined in the Introduction (p. 196).

Little more can be said about *Venjukovia* until a full description is published, since the present authors do not have access to the type specimens.

Otsheria netzvetajevi is another Russian taxon that has been implicated in dicynodont evolution. It is from the Ocher deposits (early Upper Permian) and was described by Tchudinov (1960). It resembles *Venjukovia* in certain respects, such as preorbital shortening and the emarginated zygoma, and these features indicate dicynodont affinity. The lateral pterygoid process is stronger in *Otsheria* and the palatine is not incorporated into the secondary palate, but the premaxilla extends further back to produce an incipient secondary palate.

As with *Venjukovia*, primary type material could not be examined and, although *Otsheria* is here considered to be related to the rest of the Dicynodontia, precise relationships cannot be determined at present.

Character suites

The following character suites were drawn up for each of the major genera described earlier. Each suite is designated with a letter and these letters appear on the suggested cladogram along the relevant line as depicted in Figure 40. All characters noted are thought to represent characters derived with respect to

Venjukovia, except suite A, which represents the characters of *Venjukovia* that are derived with respect to primitive therapsids.

At certain points tentative functional explanations for the changes in morphology are given.

Suite A

(i) Preorbital shortening,
(ii) the lateral pterygoid process reduced and anteriorly directed,
(iii) emargination of the zygoma,
(iv) loss of the coronoid bone,
(v) jaw articulation that permits a sliding action,
(vi) presence of a mandibular fenestra.

These features are probably related to the adoption of a herbivorous diet and to the need to increase the moment arm of the jaw adductor musculature. In contrast to other therapsids, dicynodonts have increased the moment arm not by the acquisition of a coronoid process (DeMar & Barghusen 1973) but by forward migration of the adductor insertion. This innovation is probably the key to understanding the specialized morphology of the dicynodont skull. Migration of the adductor insertion has consequences on skull structure, such as shortening of the tooth row and encroachment of the jaw musculature on the preorbital region, which are avoided if a coronoid process develops. These consequences seem to have been accepted in the dicynodont skull and capitalized upon to produce a masticatory mechanism that is suited to herbivorous feeding (King 1981).

The lateral pterygoid process might have been reduced as a consequence of, or as a prerequisite to, modification of the area of origin of the posterior pterygoideus muscle. In early therapsids such as *Titanophoneus*, the pterygoideus musculature attached to the quadrate rami of the pterygoids, and also to the posterior surfaces of the lateral pterygoid processes (Barghusen 1976). Barghusen argues that the anterior pterygoid processes of dicynodonts are modified (i.e. anteriorly directed) lateral pterygoid processes and assumes that the origin of the pterygoideus musculature is carried forward as the lateral pterygoid process is modified. A more anterior origin will enhance the forward-pulling component of this muscle, provided that the insertion remains approximately in the same position. The forward component of the pterygoideus musculature plays an important part in the masticatory cycle in protracting the jaw (King 1981) and in stabilizing the jaw articulation (Crompton & Hotton 1967).

Suite B

(i) Loss of teeth on anterior part of maxilla,
(ii) medial migration of postcanine teeth,
(iii) shallow longitudinal depression on dorsal surface of dentary,
(iv) vomers form anterior part of interpterygoidal vacuity,

(v) palatines enlarged and form part of secondary palate,
(vi) articular-quadrate joint elaborated to permit extensive sliding action
(vii) medial articular condyle enlarged,
(viii) reduction of preorbital region carried further,
(ix) temporal fenestra elongated,
(x) zygoma further emarginated,
(xi) development of a plate-like lateral extension of squamosal,
(xii) dentary with built-up area on its lateral surface for insertion of the adductor musculature.

Features (i) to (iii) are associated with the acquisition of the dicynodont horny beak, and features (iv) and (v) with the beginning of the secondary palate. Features (vi) and (vii) probably reflect the elaboration of the dicynodont masticatory pattern so that an extensive sliding action is permitted, but at the same time the medial articular condyle is enlarged to help prevent dislocation of the jaw-hinge (King 1981). Features (viii) to (xii) reflect the acquisition of the typical dicynodont pattern of jaw musculature with a branch of the adductor externus originating from the external surface of the zygoma, and a branch originating more medially from the temporal region of the skull. The insertion of the lateral branch would have been on the built-up lateral surface of the dentary (Cluver 1975; Crompton & Hotton 1967; King 1981).

All the features may be seen in the context of improving the masticatory system as an adaptation to the efficient mastication of plant material.

Suite C (defining Eodicynodon)

(i) Further loss of premaxillary teeth,
(ii) palatal exposure of the palatine bulbous and rugose,
(iii) mid-ventral palatal plate of the vomers swollen posterior to its junction with medial premaxillary process,
(iv) pterygoids extended ventrally into a powerful rugose boss anterior to internal carotid artery foramina,
(v) built-up area on dentary elaborated into a dorsal ledge projecting above general surface of jaw ramus,
(vi) cleft in maxillary rim anterior to canine tusk.

Suite D

(i) Premaxillae fused,
(ii) lateral pterygoid process reduced,
(iii) insertion of lateral external adductor migrates forward,
(iv) stapedial foramen lost.

This stage represents further elaboration of the horny beak as more teeth are lost. There is also further increase in the bite force as the insertion of the adductor externus lateralis migrates anteriorly.

Reduction of the lateral pterygoid process may reflect a further modification in the area of origin of the pterygoideus muscles, or it may indicate a

reduced role in the process of the bracing and control of movement of the lower jaw (Barghusen 1976). This control might have been less essential since the foodstuff ingested would have been passive and (more importantly) because muscles were taking over the role of controlling jaw movements.

Suite E (defining Endothiodon)

(i) Teeth lie in a row posterior to the caniniform process, with the anterior teeth on the premaxilla,
(ii) intertemporal region with postorbitals overlapping parietals,
(iii) front margin of palate bears deep median notch,
(iv) secondary palate vaulted,
(v) groove lateral to upper tooth row,
(vi) anterior portion of lower jaw forms a sharp beak,
(vii) lower jaw bears long teeth in a row,
(viii) lower jaw bears dorsal dentary trough lateral to tooth row.

Suite F

(i) Premaxillary teeth lost,
(ii) palatines extended medially and become incorporated into the rear of the secondary palate.

Suite G

(i) Longitudinal groove in dorsal edge of dentary modified into a deep, thin-walled sulcus.

The real function of this groove is at present obscure but it is most probably implicated either with the attachment of the horny beak (King 1981) or with the adductor muscle insertion (Crompton & Hotton 1967; Cluver 1971). In either case it would be involved with improvement of the feeding mechanism.

Suite H (defining Pristerodon)

(i) Built-up area on dentary enlarged into prominent dentary shelf,
(ii) palatine large and leaf-like and receives bite of lower teeth,
(iii) palatal teeth arranged in short row at an angle to longitudinal axis of palate.

Suite I

(i) Dentary built up dorsally into tables in front of dentary sulcus,
(ii) maxillary rim extended ventrally, forming a close fit with lower jaw symphysis when closed,
(iii) anterior premaxillary ridges present.

These changes probably represent adaptations to a feeding pattern with precise cutting and crushing actions between upper and lower beaks.

The palatal area (including the palatines) is also used for mastication.

Suite J

(i) Postcaniniform crest present,
(ii) nasal bosses present.

The extension of the palatal rim posteriorly as a sharp-edged crest could be involved with mastication either by increasing the length of the cutting edge between upper and lower beaks or by providing attachment for a muscular cheek that would help to retain partly chewed plant matter during mastication (Cluver 1975).

Suite K (defining Tropidostoma)

(i) Postorbitals overlap parietals, producing a narrow intertemporal region, where the parietal exposure lies within a groove.

Many specimens of *Tropidostoma* are tuskless but retain the other features of the genus. It is not clear whether this constitutes a sexual dimorphism or not.

Suite L

(i) Postcanine teeth lost,
(ii) tusks lost,
(iii) vomerine trough closes and vomerine septum becomes narrow.

The second feature may be related either to loss of a secondary sexual feature or with modification of the feeding mechanism perhaps associated with the complete loss of the postcanine teeth.

Suite M (defining Rhachiocephalus)

(i) Increase in size,
(ii) presence of a pineal boss,
(iii) narrow intertemporal region with postorbitals tending to meet behind the pineal boss.

Suite N (defining Oudenodon)

(i) Anterior extension of the interpterygoidal vacuity short, vomerine septum short.

Suite O

(i) Labial fossa present,
(ii) postcanine teeth lost,
(iii) vomerine septum narrow,
(iv) intertuberal ridge present.

Suite P (defining Aulacephalodon)

(i) Parietal with wide exposure on skull roof,
(ii) postorbital narrow and closely applied to the steep-sided intertemporal bar,

(iii) elaborate nasal bosses present,
(iv) skull broad,
(v) zygoma bears boss,
(vi) spur of jugal ascends into postorbital bar.

Pelanomodon is very similar to *Aulacephalodon* except that it is tuskless and has lost the anterior palatal premaxillary ridges. The exact relationship to *Aulacephalodon* has not yet been determined.

Suite Q (defining Dicynodon)

(i) Narrow intertemporal region,
(ii) palatal exposure of palatine flat,
(iii) lower jaw bears lateral dentary ledge.

Triassic representatives of the *Dicynodon* line.

Genera such as *Lystrosaurus*, *Kannemeyeria*, etc., possess features of the *Dicynodon* line and have their own derived features:

(i) Basicranial axis shortened,
(ii) snout deepened,
(iii) snout lengthened,
(iv) overall size increased.

Suite R

(i) Size of palatal exposure of palatine reduced,
(ii) marginal postcanine teeth lost.

The palatine area was probably not used so extensively for mastication, which instead took place on the maxilla medial to the tusk or caniniform process.

Suite S

(i) Maxilla bears an embayment anterior to caniniform process or tusk.

The embayment might have arisen as a result of the maxilla being enlarged medially to form new crushing areas for the lower jaw, or it might have served for better attachment of the horny beak.

Suite T

(i) Built-up area on dentary dorsally placed and forms dentary shelf,
(ii) anterior edge of symphysis drawn up into sharp cutting edge,
(iii) vomerine septum short and narrow,
(iv) palate bears grooves either side of median pre-maxillary ridge.

Suite U

(i) Teeth of upper jaw reduced,
(ii) anterior rami of pterygoids straight and elongate,
(iii) basicranial region shortened.

Suite V (defining Myosaurus)

(i) Absence of teeth in upper and lower jaws,
(ii) medial extent of palatine small so that palatine is confined to lateral border of choanal depression,
(iii) anterior border of orbit extends inward to close off back of snout.

Suite W (defining Emydops)

(i) Palatal exposure of palatine a flat, horizontal plate with concave posterior border.

Suite X (defining Cistecephalus)

(i) Palatines reduced posteriorly and premaxilla extends back beyond root of zygoma,
(ii) stapedial foramen present,
(iii) fossae present at the base of zygoma,
(iv) interpterygoid vacuity reduced or lost,
(v) skull roof wide,
(vi) teeth absent.

Suite Y

(i) Maxillary embayment extended into a notch,
(ii) dorsal longitudinal dentary groove lost,
(iii) maxillary rim extended ventrally to form caniniform process.

Suite Z (defining Diictodon)

(i) Absence of postcanine teeth,
(ii) anterior part of palatal exposure of palatines greatly reduced,
(iii) dentary table prominent with medial edge built up higher than lateral edge,
(iv) built-up area on lateral surface of dentary weak and low down on jaw,
(v) anterior palatal ridges present,
(vi) postorbitals overlap parietals producing a narrow intertemporal region,
(vii) caniniform process blade-like,
(viii) ventral keel on anterior pterygoid ramus.

Suite A^1 (defining Robertia)

(i) Built-up area on lateral surface of dentary ledge-like and occludes mandibular fenestra.

Suite B¹ (defining Kingoria)

(i) Absence of postcanine teeth,
(ii) dentary shelf large,
(iii) dorsal edge of lower jaw sharp,
(iv) palatal exposure of palatine reduced so that it is confined to lateral border of choana,
(v) mandibular fenestra closed up,
(vi) lower beak sharp and shovel-shaped,
(vii) thin plate-like ventral extension to anterior pterygoid ramus,
(viii) maxilla bears ventral keel posterior to caniniform process.

A cladogram (Fig. 40) has been drawn up, using the character suites set out above.

Fig. 40. Cladistic interpretation of the relationships between Permian Dicynodontia.

A CLASSIFICATION OF DICYNODONTS

In erecting the following classification from the cladogram, each successive group diverging from the main axis (A–B¹) has been given equal rank as a suborder. Along each main divergent line secondary divergent lines have been given the rank of superfamily, tertiary lines that of family, and quaternary lines that of subfamily.

This sequential method of classification has been used, first, because the detailed taxonomic picture of dicynodonts is far from complete and, secondly, because any classification should be able to accommodate newly discovered specimens. It should be possible to add other taxa to this classification at a future date without disturbing its hierarchical order. This procedure also obviates the necessity of proposing several completely new taxon names.

Some notes are necessary concerning the use of the term Dicynodontia instead of Anomodontia, the raising of the Dicynodontia to subordinal status, and the inclusion of the Venjukoviamorpha within the Dicynodontia.

Owen (1859) erected the order Anomodontia for animals without teeth (except possibly tusks or caniniform processes) with a parietal foramen, two nostrils, and a fixed tympanic pedicle. He included three families within the order: the Dicynodontia (*Dicynodon* and *Ptychognathus* = *Lystrosaurus*), the Cryptodontia (*Oudenodon*), and the Gnathodontia (*Rhynchocephalus*).

In 1861 Owen modified this classification, excluding the Gnathodontia and including the Cynodontia for forms such as *Galesaurus*. Owen in 1876 again modified this classification, renaming the Dicynodontia the Bidentalia and including only this family, the Dicynodontia, and a new family the Endothiodontia (for *Endothiodon*).

Seeley (1889, 1894), Lydekker (1890), and Nicholson & Lydekker (1899) included further families within the Anomodontia, but Broom (1905) stressed that many of these families did not fall within the original definition that Owen used for the Anomodontia, and suggested that only forms allied to *Dicynodon* (i.e. *Oudenodon*, *Lystrosaurus*, etc.) should be included.

Broom's (1905) classification of Therapsida stood with little change until the classification of Watson & Romer (1956). These authors divided the Therapsida into the Theriodontia and the Anomodontia, which included the 'dicynodonts' (equivalent to Broom's (1905) Anomodontia), the dromasaurs, and the herbivorous dinocephalians. A new infraorder, the Dicynodontia, was erected within the suborder Anomodontia. The present authors feel that the evidence for dividing the herbivorous from the carnivorous dinocephalians, and for associating the herbivorous forms with the dicynodonts is very inconclusive, and propose that all dinocephalians be retained within the taxon Dinocephalia and that this taxon and the Dicynodontia be considered as independent suborders of the order Therapsida. It is further suggested that since the term Dicynodontia is now in common usage it be used in preference to Anomodontia, which would become a *nomen nudum*.

Venjukovia has been included (with *Otsheria*) in the infraorder Venjukoviamorpha (Romer 1966). This infraorder has equal ranking with the Dicynodontia in Romer's classification. It was argued earlier in the present work that *Venjukovia* exhibits features that link it closely with dicynodonts and that it should be included within the Dicynodontia. Accordingly, the infraorder Venjukoviamorpha is here included in the suborder Dicynodontia.

Order THERAPSIDA

Suborder DICYNODONTIA nov.	
Infraorder VENJUKOVIAMORPHA Romer, 1966	*Venjukovia* Efremov, 1940 *Otsheria* Tchudinov, 1960
Infraorder EODICYNODONTIA nov.	*Eodicynodon* Barry, 1974
Infraorder ENDOTHIODONTIA nov.	*Endothiodon* Owen, 1876 *Pachytegos* Haughton, 1932 *Chelydontops* Cluver, 1975
Infraorder PRISTERODONTIA nov.	
Superfamily DICYNODONTOIDEA nov.	
Family **Cryptodontidae** Owen, 1859	
Subfamily Tropidostominae nov.	*Tropidostoma* Seeley, 1889
Subfamily Pelorocyclopinae van Hoepen, 1934	*Rhachiocephalus* Owen, 1876
Subfamily Oudenodontinae nov.	*Oudenodon* Owen, 1869
Family **Aulacephalodontidae** nov.	
Subfamily Aulacephalodontinae Toerien, 1953	*Aulacephalodon* Owen, 1844
Subfamily Pelanomodontinae nov.	*Pelanomodon* Broom, 1938
Family **Dicynodontidae** Owen, 1859	*Dicynodon* Owen, 1845
Family **Kannemeyeriidae** von Huene, 1948	Triassic forms
Family **Pristerodontidae** nov.	*Pristerodon* Huxley, 1868 *Emyduranus* Broom, 1921 *Synostocephalus* Broili & Schröder, 1935
Infraorder DIICTODONTIA nov.	
Superfamily EMYDOPOIDEA nov.	
Family **Emydopidae** nov.	
Subfamily Emydopinae nov.	*Emydops* Broom, 1912
Subfamily Myosaurinae nov.	*Myosaurus* Haughton, 1917 *Myosauroides* Broom, 1941
Family **Cistecephalidae** Toerien, 1953	*Cistecephalus* Owen, 1876 *Cistecephaloides* Cluver, 1974*a* *Kawingasaurus* Cox, 1972
Superfamily ROBERTOIDEA nov.	
Family **Robertiidae** nov.	*Robertia* Boonstra, 1948
Family **Diictodontidae** nov.	*Diictodon* Broom, 1913
Infraorder KINGORIAMORPHA nov.	*Kingoria* Cox, 1959 *Kombuisia* Hotton, 1974

Incertae sedis

Gordonia Newton, 1893 (possibly related to *Kingoria* or *Dicynodon*)
Eosimops newtoni Broom, 1921
Cryptocynodon simus Seeley, 1894
Koupia Boonstra, 1948
Brachyuraniscus Broili & Schröder, 1935
Broilius Toerien, 1953
Ceraetulurus mirabilis Broom, 1931
Palemydops Broom, 1921 (related to *Emydops*)
Aulacocephalus pithecops Seeley, 1898
Compsodon helmoedi van Hoepen, 1934
Eurychororhinus boonstrai Broili & Schröder, 1935 (possibly *Pristerodon*)
Prodicynodon Broom, 1904 (possibly related to *Endothiodon* or *Chelydontops*)
Taognathus megalodon Broom, 1911
Eumantellia mirus Broom, 1911
Newtonella platyceps Broom, 1937
Heuneus oudebergenis Toerien, 1953

Premaxillary teeth have been recorded in *Eumantellia*, *Newtonella* and *Heuneus*. If correct, this will warrant a new infraorder. However, it is more likely that these are maxillary teeth that happened to erupt through the premaxilla. Little more can be said about the status of these forms until more material has been prepared.

Parringtoniella broomi Toerien, 1953
Emydorhinus fragilis Broom, 1935 (type specimen cannot be traced)
Emydorhinus sciuroides Broom, 1921, 1935
Dicynodontoides Broom, 1940 (probably *Kingoria*, see Cluver & Hotton 1981)
Digaladon Broom & Robinson, 1948 (possibly a juvenile *Aulacephalodon*)
Haughtoniana magna Boonstra, 1938 (type specimen is indeterminate)
Anomodon Keyser, 1975 (erected on the basis of the description of *Dicynodon heunei* Broili & Schröder, 1937; may be related to *Robertia* or *Diictodon*)
Storthyggognathus Janensch, 1952 (probably related to *Pristerodon*).

CONCLUSIONS

The classification erected in the present work is considered to be definitive in that it is hoped that its major divisions will not change. However, new taxa must be incorporated as they become known or better understood and this will inevitably lead to slight modifications in the classification. The need for specific revision within the Dicynodontia remains very evident. This has not been attempted in the present work and, in addition, certain genera have been left *incertae sedis* because they are either badly preserved or inadequately prepared.

It is hoped that future modifications of the classification will be based on well-prepared primary type material.

With the establishment of a definitive classification, the groups involved can be used in a more meaningful way in ecological, palaeogeographical, and functional anatomical contexts.

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ABBREVIATIONS

add. fos.	adductor fossa
ang.	angular
art.	articular
b.	boss
bas.	basisphenoid
boc.	basioccipital
den.	dentary
den. gr.	dentary groove
den. s.	dentary sulcus
den. t.	dentary table
ect.	ectopterygoid
eoc.	exoccipital
ept.	epipterygoid
for. mag.	foramen magnum
fr.	frontal
ioc.	canal for internal carotid artery
ip.	interparietal
ipt. vac.	interpterygoid vacuity
itr.	intertuberal ridge
jug.	jugal
lab. fos.	labial fossa
lac.	lacrimal
lat. pal. f.	lateral palatal fenestra
l.s.	lateral shelf
max.	maxilla
max. gr.	maxillary groove
no.	notch
op.	opisthotic
orb.	orbitosphenoid
pa.	parietal
pal.	palatine
pas.	parasphenoid
poc.	postcaniniform crest
pfr.	prefrontal
pm.	premaxilla
po.	postorbital
pof.	postfrontal
pp.	preparietal
pro.	prootic

pres.	presphenoid
pt.	pterygoid
pt. f.	posttemporal fenestra
q.	quadrate
q.j.	quadratojugal
ref. l.	reflected lamina
sa.	surangular
smx.	septomaxilla
soc.	supraoccipital
sq.	squamosal
st.	stapes
t.	tusk
to.	tooth
tab.	tabular
vo.	vomer
VII f.	foramen for facial nerve
AMNH	American Museum of Natural History
BMNH	British Museum (Natural History)
ROZ	Roy Oosthuizen Collection, South African Museum
SAM	South African Museum

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype
SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

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&
GILLIAN M. KING

A REASSESSMENT OF THE RELATIONSHIPS OF PERMIAN DICYNODONTIA (REPTILIA, THERAPSIDA) AND A NEW CLASSIFICATION OF DICYNODONTS